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*Cover design:* The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor). The Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).



## An introduced parasite, *Lernaea cyprinacea* L., found on native freshwater fishes in the south west of Western Australia

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### Abstract

*Lernaea cyprinacea* L. is a parasitic copepod found on the skin and gills of freshwater fishes. Although *L. cyprinacea* has been introduced into eastern Australia, it has, until now, never been reported in Western Australia. We found infestations of *L. cyprinacea* on four native fish species (*Galaxias occidentalis* Ogilby; *Edelia vittata* Castelnau; *Bostockia porosa* Castelnau; *Tandanus bostocki* Whitley) and three introduced fish species (*Carassius auratus* L.; *Gambusia holbrookii* (Girard); *Phalloceros caudimaculatus* (Hensel)) at two localities in the Canning River, in the south west of Western Australia. The likely source of the parasites is introduced cyprinids, such as *C. auratus* and *Cyprinus carpio* L. The parasite has the potential to have serious pathogenic effects on native fish species, although it appears to be currently localised to a small section of the Canning River.

**Key words:** freshwater fish, parasite, *Lernaea*, Western Australia

### Introduction

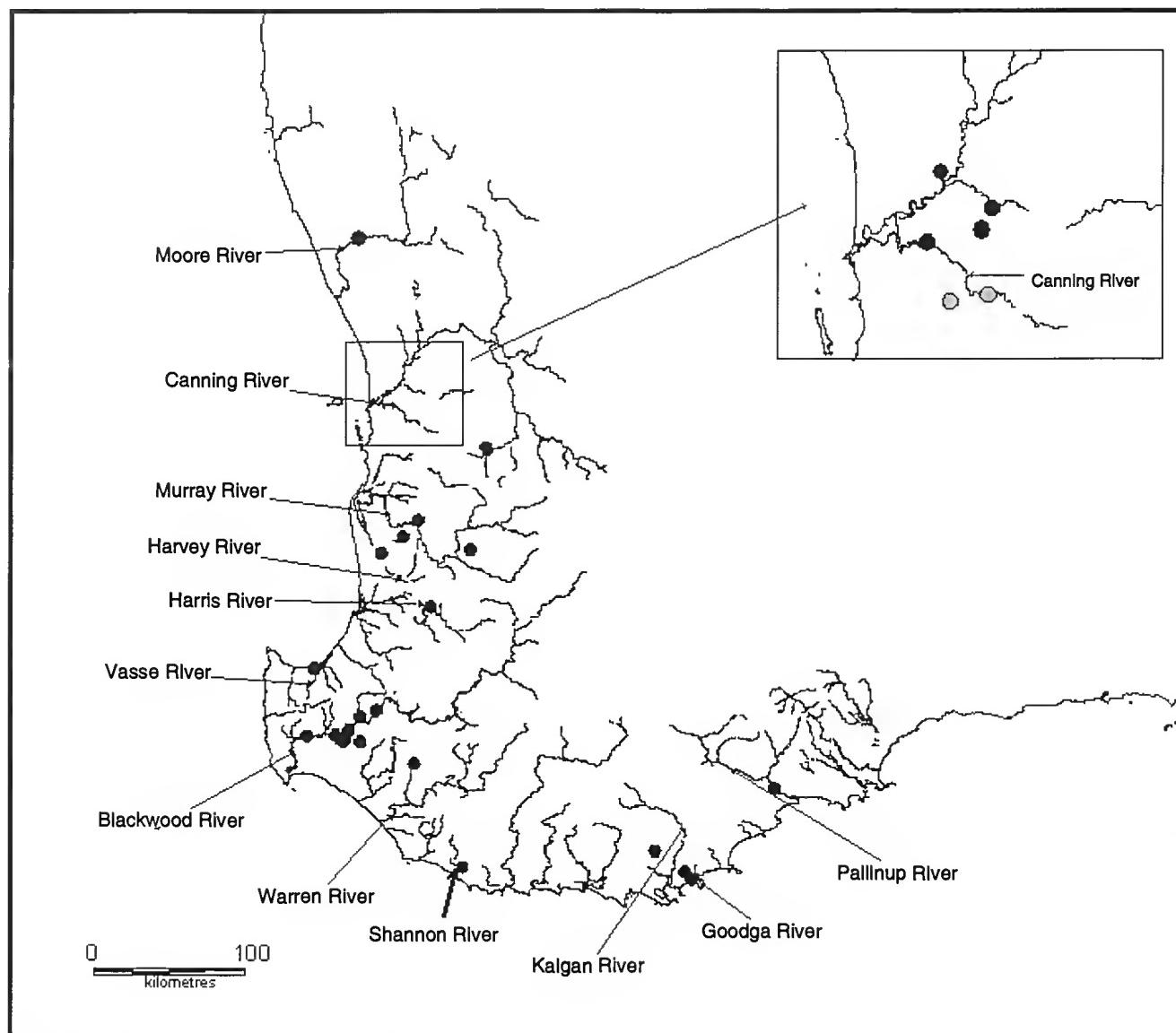
The South West Coast Drainage Division (Figure 1) contains a depauparate, but highly endemic freshwater fish fauna, with eight of the 10 native species found in the region being endemic (Morgan *et al.* 1998). A number of exotic fish species have also been introduced into south west rivers, either deliberately or as escapees from aquaculture or the aquarium trade (Morgan *et al.* 2004). Morgan *et al.* (2004) documented a number of potentially deleterious impacts of introduced fishes on native species in the south west, including predation, competition and habitat alteration. Introduced fishes may also transfer exotic diseases to native species, and this has been an increasing cause of concern for the health of freshwater environments throughout the world (Bauer 1991; Kennedy 1993; Arthington & McKenzie 1997; Levy 2004).

Lernaeosis is a disease of freshwater fishes caused by parasitic copepods of the family Lernaeidae (anchor worms). About 110 species of lernaeids have been described in 14 different genera (Ho 1998). The most common species is *Lernaea cyprinacea* L., which has been widely translocated with cultured fish species and is now found throughout North America, Europe, Asia, southern Africa and eastern Australia (Hoffman 1970; Lester & Haywood 2006). *Lernaea cyprinacea* has a very wide host range and has been found on more than 45 species of cyprinids, as well as fishes belonging to many other orders and occasionally on tadpoles (Tidd & Shields 1963; Lester & Haywood 2006).

Although *L. cyprinacea* is not native to Australia, the parasite has been recorded from a number of native and cultured fish species in New South Wales and Victoria, in eastern Australia (Ashburner 1978; Hall 1983; Callinan 1988; Rowland & Ingram 1991; Dove 2000; Bond 2004). In this paper, we provide the first published report of *L. cyprinacea* in Western Australia.

### Methods

As part of a larger study on the parasite fauna of freshwater fishes in Western Australia, we sampled 1429 fishes of 18 different species from 29 localities in 12 rivers, spanning the extent of the South West Coast Drainage Division (Figure 1, Table 1). After *Lernaea* infestations were found at one locality in the Canning River, we sampled a further five localities in the Swan/Canning system (Figure 1). Adult and juvenile fishes were captured during summer and autumn, 2005–2007, using a combination of seine nets (3 mm mesh), fyke nets (92 mm mesh), gill nets (25–125 mm mesh) and electrofishers. Water temperature and conductivity were recorded for each locality on each sampling occasion. Fishes were returned to the laboratory, weighed and measured for total length (TL), and the skin and gills examined externally for *Lernaea* infestation using a dissecting microscope. *Lernaea* specimens were removed and preserved in 70% ethanol. After clearing in lactophenol, they were mounted whole for identification using a compound microscope. Parasite data were expressed as prevalences (proportion of infested hosts) and intensities of infestation (number of parasites per infested host). Ninety five percent confidence intervals were calculated for prevalences, assuming a binomial



**Figure 1.** Southwest Coast Drainage Division, showing sampling locations. Black circles indicate that no fishes from that location were infested with *Lernaea*, grey circles indicate that *Lernaea* were found on some sampled fishes.

**Table 1**

Number of fishes sampled from each of 12 different river systems in the South West Coast Drainage Division of Western Australia.

River system	Number of localities sampled	Number of fishes collected
Moore River	1	59
Canning River	7	441
Murray River	2	42
Harvey River	3	113
Harris River	1	20
Vasse River	1	46
Blackwood River	8	462
Warren River	1	4
Shannon River	1	7
Kalgan River	1	139
Goodga River	2	76
Pallinup River	1	20
<b>Total</b>	<b>29</b>	<b>1429</b>

distribution, and intensities, from 2,000 bootstrap replications, using the software Quantitative Parasitology 3.0 (Rózsa *et al.* 2000). Differences in size between infested and non-infested hosts were tested by analysis of variance.

## Results

Of the 12 different rivers sampled, anchor worms were found only on fishes from the Swan/Canning system. Infested fish were found at two of six localities in this system (Figure 1). Water temperatures at these localities over the sampling period ranged from 17–30°C and salinities from 2,000–4,000 mg L<sup>-1</sup>. Overall prevalences (*i.e.*, prevalences of infestation for all fish species) at the two localities were 0.06 (*n* = 63 fishes) at Soldier Crossing and 0.18 (*n* = 231 fishes) at Southern River.

Four native fish species (western minnow, *Galaxias occidentalis* Ogilby; western pygmy perch, *Edelia vittata* Castelnau; nightfish, *Bostockia porosa* Castelnau;

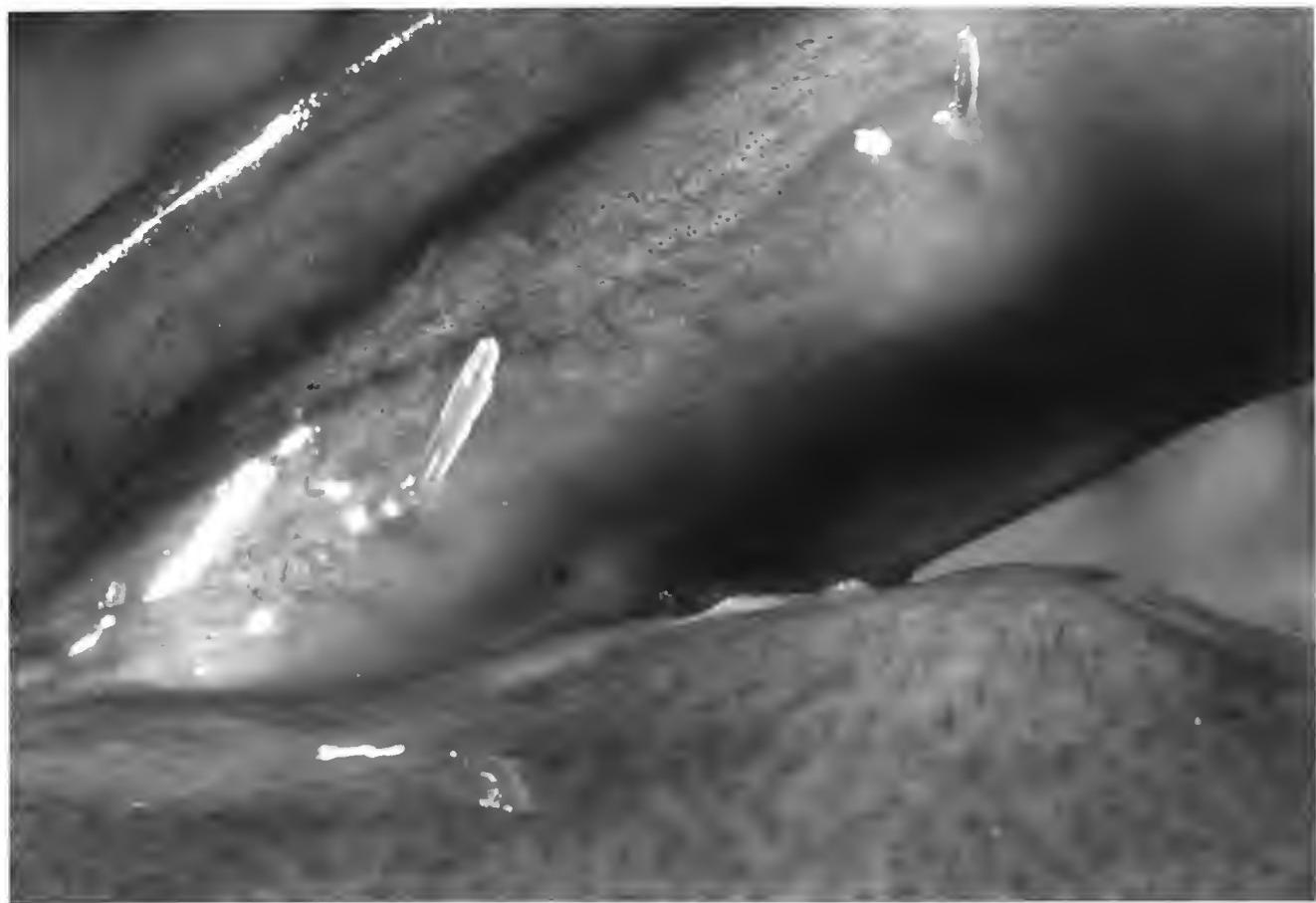


Figure 2. Ulcerated lesions at the site of attachment of female anchor worms to a freshwater cobbler (*Tandanus bostocki*) host.

freshwater cobbler, *Tandanus bostocki* Whitley) and three introduced fish species (goldfish, *Carassius auratus* L.; eastern mosquitofish, *Gambusia holbrooki* (Girard); and one-spot livebearer, *Phalloceros caudimaculatus* (Hensel)) were infested at the two localities. Prevalences differed between fish species, with the native species *G. occidentalis* and *E. vittata* being most heavily infested (Table 2). For these two species, infested fish tended to be

larger, although this difference was significant only for *E. vittata* (mean TL of infested fish = 38.5 mm, mean TL of non-infested fish = 32.2 mm,  $F_{1,73} = 6.28$ ,  $P < 0.01$ ). For the introduced *C. auratus*, infested fish were significantly smaller, although the sample size of infested fish was small (mean TL of infested fish = 75.5 mm, mean TL of non-infested fish = 104.2 mm;  $F_{1,31} = 4.04$ ,  $P < 0.05$ ).

Most infested fishes contained a single parasite, with a mean intensity over all fish species of 1.29 (95% confidence interval = 1.12–1.45; range = 1–3). Of the 45 *Lernaea* that were found, 96% were adults and 72% were attached to the base of the dorsal fin of their host, with the remainder attached to either the base of the caudal, pectoral or pelvic fins or to the general body surface. All parasites were morphologically similar to *Lernaea cyprinacea* as described by Kabata (1979).

We found extensive hemorrhages and ulceration at attachment sites in infested native fishes (Figure 2) and also captured several fishes without *Lernaea*, but with large scars at the base of their dorsal fins, which are likely to have been caused by previous infestations.

## Discussion

As far as we are aware, this is the first account of *Lernaea* infestation on fishes in Western Australia. It appears that the species in Western Australia is most likely to be *L. cyprinacea*, although the considerable morphological plasticity of species of *Lernaea*

Table 2

Prevalence (with 95% confidence interval in parentheses) of *Lernaea* infestation in seven species of fish captured at two localities in the Canning River, Western Australia.

Species	Location	N	Prevalence
<i>Galaxias occidentalis</i>	Southern River	40	0.40 (0.25–0.60)
	Soldier Crossing	20	0.00
<i>Edelia vittata</i>	Southern River	76	0.20 (0.12–0.30)
	Soldier Crossing	13	0.23 (0.07–0.52)
<i>Bostockia porosa</i>	Southern River	10	0.10 (0.00–0.48)
	Soldier Crossing	10	0.10 (0.00–0.48)
<i>Tandanus bostocki</i>	Southern River	1	1.00
<i>Carassius auratus</i>	Southern River	39	0.10 (0.04–0.24)
<i>Gambusia holbrooki</i>	Southern River	39	0.02 (0.00–0.14)
	Soldier Crossing	20	0.00
<i>Phalloceros caudimaculatus</i>	Southern River	27	0.04 (0.00–0.18)

complicates morphological identification (Kabata 1979; Lester & Haywood 2006), and definitive confirmation of species identity will require molecular genetic studies.

*Lernaea cyprinacea* has been widely distributed throughout the world, presumably through the translocation of cyprinid hosts such as *C. auratus* and European carp, *Cyprinus carpio* L. This is also the likely origin of the parasite in Western Australia, possibly through the release or escape of infested aquarium fishes into natural waterways. Morgan *et al.* (2004) have reported *C. auratus* and *C. carpio* from many streams, irrigation drains and lakes in the vicinity of Perth, and also from a number of other natural waterways between the Moore and Vasse Rivers on the Swan Coastal Plain.

We found *Lernaea* infestations on seven different species of fish, with the greatest prevalence on the native species *G. occidentalis* and *E. vittata*, rather than the natural cyprinid hosts of the parasite. Differences in infestation levels among different host species have also been reported in many other studies (e.g., Demaree 1967; Shariff *et al.* 1986; Marcogliese 1991; Bond 2004) and may result from different encounter frequencies between host and parasite, from differences in the rate of attachment of the parasite to different host species or from differences in the immune response of different host species to the parasite. At this stage, we have no information on the reason for the greater rate of infestation of *G. occidentalis* and *E. vittata*.

Our results suggest that *L. cyprinacea* is currently confined to a relatively small section of the Canning River, although future surveys around the Perth metropolitan area are necessary to confirm this. The spread from this population is likely to be slow, because of the life cycle of the parasite and the physical characteristics of the river, which is short and separated from other river systems by an extensive estuary. Female anchor worms, attached to the body of their host, produce eggs which hatch into free-living naupliar larvae. After about four days, the naupliar larvae moult to infective copepodid larvae, which attach, usually to the gills of a host fish. Copepodids moult to adults after a week or more, depending on the temperature, with optimal development occurring at 28–36°C and little development below 20°C (Shields & Tidd 1968; Marcogliese 1991; Lester & Haywood 2006). Adult males die within 24 hours and fertilised females either attach to the same host or swim to another host. Distribution and migration of the parasite in the south west is likely to be restricted by the direct life cycle, temperature-dependent development, low salinity tolerance and reduced survival in fast-flowing water (Bulow *et al.* 1979; Medeiros & Maltchik 1999; Lester & Haywood 2006).

*Lernaea* infestations can have serious pathogenic effects on their fish hosts. Copepodites may cause disruption and necrosis of gill epithelium, while attachment of adult females usually causes hemorrhages, muscle necrosis and an intense inflammatory response, sometimes associated with secondary bacterial infections (Khalifa & Post 1976; Berry *et al.* 1991; Lester & Haywood 2006). Bond (2004) demonstrated high mortality rates and reduced swimming ability, which might predispose to greater predation rates, in two species of native eastern Australian freshwater fish (*Galaxias olidus* Günther and *Nannoperca australis* Günther) infested with *Lernaea*.

There is evidence that the pathological effects of *Lernaea* infestations are greater on smaller fish because the attachment organ of the parasite penetrates more deeply into the body of the fish, often causing damage to internal organs (Khalifa & Post 1976; Lester & Haywood 2006). Most native freshwater fishes in the south west of Western Australia are much smaller than typical cyprinid hosts, and the greater prevalence of infestation on larger native fishes in our study may result from an increased mortality rate of infested small native fishes, although this is speculative and remains to be tested experimentally.

Elimination of *Lernaea* from the Canning River is not likely to be achieved. Although the parasite appears to be relatively confined, it has spread to a number of different fish species, both native and introduced. A number of chemical treatments are effective against copepodids (although less effective against embedded adults or nauplii), and in a closed culture system these can be applied over a number of weeks to break the life cycle of the parasite (Lester & Haywood 2006). In an open, natural river system this is not a feasible proposition. The best prospect for containing the spread of the parasite is to prevent future releases of infected hosts into other river systems. This will require an extensive education campaign to alert the public to the threat posed by this, and other exotic diseases, which may be associated with aquarium fishes.

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# Fishes and freshwater crayfishes of major catchments of the Leschenault Estuary: Preston and Brunswick River, including first record of a freshwater gudgeon (Eleotridae) from south-western Australia

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## Abstract

A paucity of information exists on the fish and crayfish communities of two major rivers that flow into the Leschenault Inlet, south-western Western Australia. This study documents these communities and assesses their ecological significance. During February 2006, seven sites were sampled for fish and freshwater crayfish on each of the Brunswick River and Preston River with additional sites having been previously sampled in the summer of 1999/2000. The rivers generally had similar native fish communities with four endemic species, Freshwater Cobbler, Western Minnow, Western Pygmy Perch and Nightfish making up 60% of all fish captures (2670) with the remaining being from three feral freshwater and six estuarine species. Two native species of freshwater crayfish were also recorded, the Marron and Gilgie. The endemic Western Minnow and Western Pygmy Perch were the most common and widespread native fish species in both rivers. This study recorded what appears to be the Empire Gudgeon in the Preston River; the first record of this northern Australian species in the South-west Drainage Division, and its presence was attributed either to marine larval drift or as a result of an aquarium release. The potential impact of instream barriers on native fish migrations in these systems is discussed.

**Keywords:** freshwater fish, freshwater crayfish, Leschenault Estuary, Preston River, Brunswick River, south-west Australia.

## Introduction

The Leschenault Inlet, located on southern Western Australia's Swan Coastal Plain near Bunbury receives discharge from the Brunswick, Collie, Preston and Ferguson Rivers. There is a considerable amount of information detailing the fish fauna of the Leschenault Inlet with Potter *et al.* (1997, 2000) recording 42 species of fish from 26 families. The estuary is dominated by gobies, atherinids and clupeids which comprised almost 90% of the fishes. Potter *et al.* (2000) also reported 13 species from gill net captures in the lower (tidal) Collie River. Neither of these studies reported on the fishes found within the freshwaters of the Leschenault Inlet catchment and although Pen & Potter (1990, 1991a, 1991b, 1991c, 1991d, 1992) conducted biological studies on a number of native and introduced freshwater fishes in the upper Collie River, there is no published information regarding the fishes (or freshwater crayfishes) of the Brunswick or Preston Rivers.

The distributions of fishes inhabiting the inland waters of the south-western corner of Western Australia were documented in Morgan *et al.* (1998) and include the systems from Capel to Two People's Bay east of Albany and thus does not encompass the more northerly

Leschenault catchments, but does include some sites on the Collie River South Branch. The aims of the present study were to document the freshwater fishes and crayfishes of the Brunswick and Preston rivers and ameliorate the paucity of knowledge of the fishes and freshwater crayfishes inhabiting two of the major systems flowing into the Leschenault Inlet.

## Methods

During February 2006, seven sites were sampled for fish and freshwater crayfish on each of the Brunswick River and Preston River (Fig. 1). An additional eight sites were sampled for freshwater fish in the Brunswick and Preston Rivers by the senior author in the summer of 1999/2000 (Fig. 1).

The sampling regime for fish and freshwater crayfish aimed at determining the densities of each species present at each site over an area of up to 340 m<sup>2</sup>. A range of in-stream habitats at each site was sampled to account for differential use of micro-habitats by the prevailing species. At each site, stop nets were set upstream and downstream to block the escape of animals from the stream section. A combination of double-pass back-pack electrofishing (*Smith-Roof Model 12-A*) and a variety of seine nets (in deeper habitats) were then deployed to record all animals in the stream section.

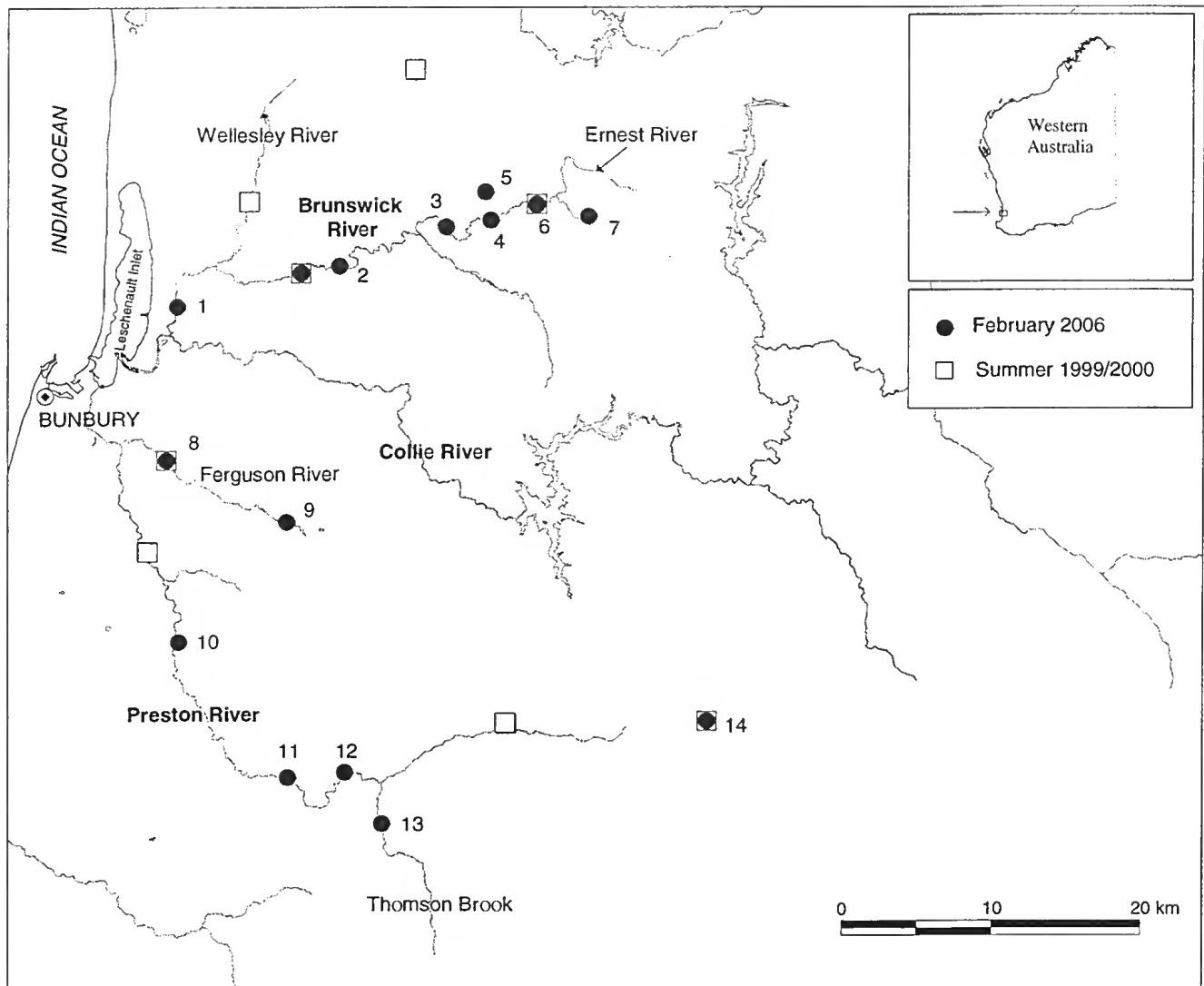


Figure 1. Sites sampled for fish and freshwater crayfish in the Brunswick and Preston Rivers.

Upon capture, all were identified, measured to the nearest 1 mm total length (TL) (for fish) or orbital carapace length (OCL) (for freshwater crayfish) and then promptly released. The density of each species at each blocked section was then determined.

## Results

### Fish species captured

A total of 1336 and 1334 fish were captured in the Brunswick and Preston Rivers, respectively. Within the Brunswick River however, 529 fish were from five estuarine species that were captured in a tidally influenced site. To allow comparisons between the fauna in the different systems we exclude this site and focus on those fishes captured at sites upstream of tidal influence.

### Freshwater Endemic Fishes

During this study four of the eight species of freshwater fish endemic to south-western Australia were found within the catchments that drain into the Leschenault Inlet, including the Freshwater Cobbler

(*Tandanus bostocki* Whitley, 1944), Western Minnow (*Galaxias occidentalis* Ogilby, 1899), Western Pygmy Perch (*Edelia vittata* Castelnau, 1873) and Nightfish (*Bostockia porosa* Castelnau, 1873) (Fig. 2).

Freshwater Cobbler was found in both the Brunswick (five fish from three sites) and Preston (four fish at one site) rivers and it is also known to be common throughout the Collie River, including Wellington Dam (Fig. 2). Within the Preston River it was only found at site 10 below the gauging station weir in Boyanup (Figures 1 and 2).

The Western Minnow was found to be widespread throughout both the Brunswick and Preston Rivers (Fig. 2). Within the Brunswick River our catches were dominated by larger (>1 year old) fish with only one fish <70 mm TL captured. In contrast, within the Preston River large numbers of new recruits (0+) were captured.

The Western Pygmy Perch was found to be widespread throughout both the Brunswick and Preston Rivers (Fig. 2). Similar to the Western Minnow, the population of Western Pygmy Perch within the Brunswick River was dominated by larger (>1 year old)

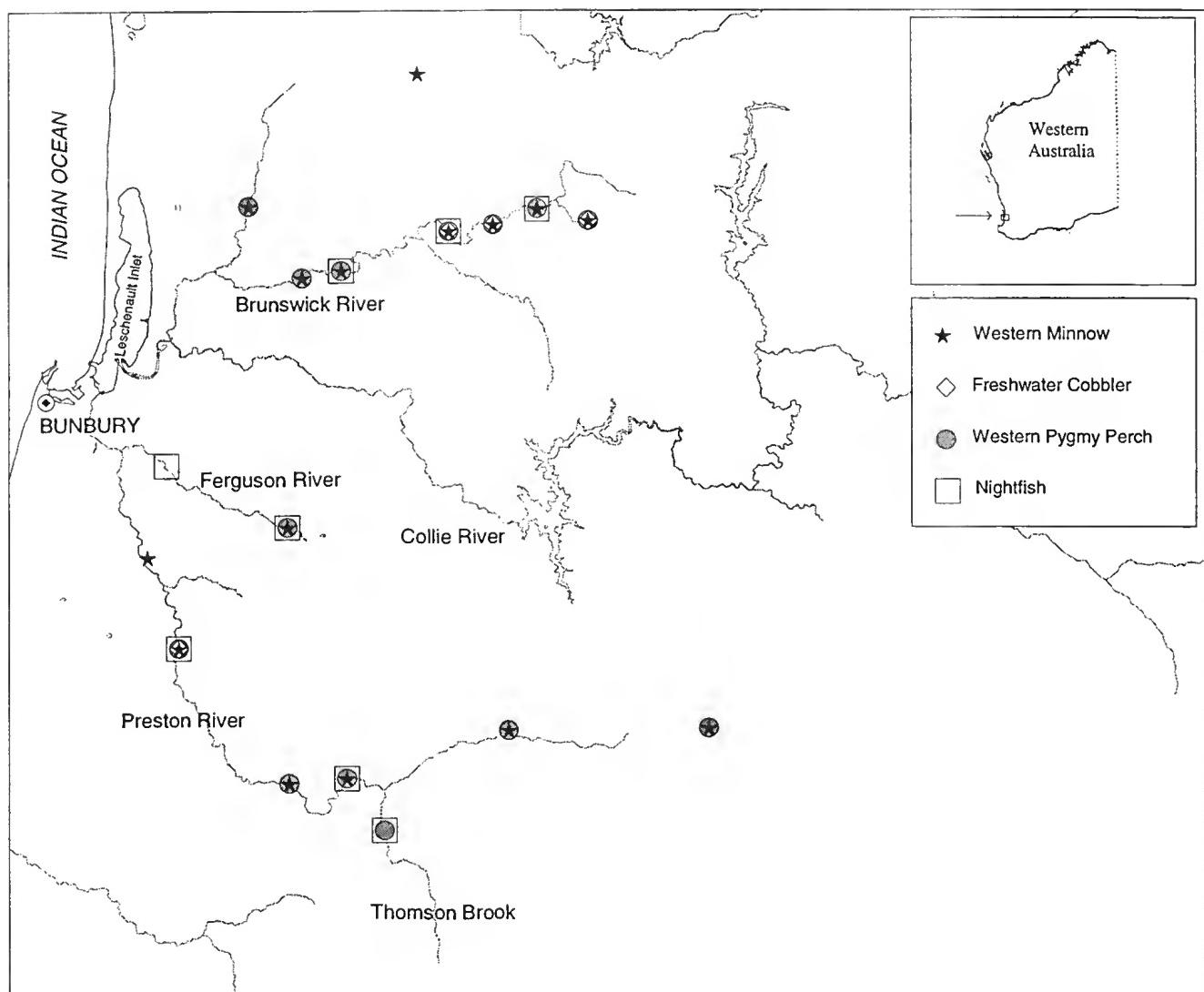


Figure 2. Capture locations of endemic freshwater fishes in the Brunswick and Preston Rivers.

fish with far greater recruitment occurring in the Preston River where large numbers of new recruits (0+) were captured. The species was captured up to a size of 60 mm TL in both the Brunswick and Preston rivers.

The Nightfish was found to be widespread throughout the Preston River but was restricted to the headwaters of the Brunswick River (Fig. 2). While a number of larger individuals were captured (up to ~150 mm TL and 140 mm TL in the Brunswick and Preston Rivers, respectively) many new recruits were also caught.

#### *Estuarine fishes in the freshwaters*

Within the Brunswick River the marine/estuarine opportunistic Yellow-eye Mullet (*Aldrichetta forsteri* (Valenciennes, 1836)) and Whitebait (*Hyperlophus vittatus* (Castelnau, 1875)) and the marine straggler Blue Sprat (*Spratelloides robustus* Ogilby, 1897) were captured at the limit of tidal influence, as were the typically estuarine Western Hardyhead (*Leptatherina wallacei* Prince, Ivantsoff & Potter, 1982), the Swan River Goby (*Pseudogobius olorum* (Sauvage, 1880)) and the South-western Goby (*Afurcagobius suppositus* (Sauvage, 1880)). While these species were not found in the

freshwater environment of the Brunswick River; both the South-western Goby and the Western Hardyhead were captured in the freshwaters of the Preston River.

During this study we captured what appeared to be an Empire Gudgeon [*Hypseleotris compressa* (Kraefft, 1864)] (Fig. 3) at site 10 downstream of the gauging station weir at Boyanup on the Preston River (Fig. 1). In agreement with published morphological counts of the species in Hoese & Allen (1983), the 33 mm TL individual captured in the Preston River had: 2 pores on the preoperculum; 1<sup>st</sup> dorsal fin rays – VI; 2<sup>nd</sup> dorsal fin rays – I, 9; anal fin rays – I, 10; and an elongate vertical dark spot just below the base of the caudal fin.

#### *Introduced Fishes*

During this study we captured three introduced fishes, including: two Goldfish (*Carassius auratus* Linnaeus, 1758) from the Preston River at site 10 below the gauging station at Boyanup; a number of Rainbow Trout (*Oncorhynchus mykiss* (Walbaum, 1792)) from the upper Brunswick River; and Eastern Mosquitofish (*Gambusia holbrooki* (Girard, 1859)) from numerous sites throughout both systems (Figures 1 and 4).



Figure 3. The Empire Gudgeon (*Hypseleotris compressa*) captured in the Preston River.

#### Freshwater crayfish species captured

Two species of freshwater crayfish were captured during this study, the Gilgie (*Cherax quinquecarinatus* Gray, 1845) and the Marron (*Cherax cainii* Austin and Ryan, 2002) (Fig. 5). While the Gilgie was extremely widespread and often found in high densities, the Marron was less abundant and somewhat restricted (Fig. 5). For example, of the 269 and 335 freshwater crayfish captured in the Brunswick and Preston rivers, respectively, Gilgies represented ~97–98% of the catch in these systems.

#### Discussion

The Preston and Brunswick rivers were found to have very similar fish and crayfish communities. For example, approximately 60% of the fish captured in both rivers were from four freshwater fish species that are endemic to south-western Australia. Pen & Potter (1990, 1991a, b, c) and Morgan *et al.* (1998) also reported these species from the Collie River. The majority of the remaining fishes captured in the Brunswick and Preston rivers consisted of two and three introduced species, respectively.

The gauging station weir at Boyanup on the Preston River (site 10), and the weir at Brunswick Junction on the Brunswick River (site 2), had high congregations of the endemic species and it is likely that these weirs severely impact on the upstream migrations of many species within the river. For example, the Freshwater Cobbler

undertakes upstream spawning migrations during late spring and summer and barriers would significantly impact on such movements. These barriers could be overcome with the construction of fishways such has recently occurred in other rivers in the region such as the Goodga River (Morgan & Beatty 2006) and Margaret River (Beatty *et al.* 2007).

The study recorded relatively large adult sizes of a number of endemic species; specifically the Western Minnow, Western Pygmy Perch and Nightfish. For example the maximum size of the Western Pygmy Perch is ~70 mm TL (Pen & Potter 1991c) and in the Brunswick and Preston Rivers they were captured up to 60 mm TL. Furthermore, the maximum size of the Nightfish is considered to be ~160 mm TL (Allen 1982) and fish within the Brunswick and Preston Rivers were caught approaching this size, *i.e.* up to ~150 mm TL and 140 mm TL, respectively. Therefore, in contrast to many rivers of the region that have been considerably altered by salinisation, eutrophication and/or river regulation (Morgan *et al.* 1998), these rivers appear to provide continuous flows and suitable permanent habitats that may have resulted in these species having high longevities.

A number of marine/estuarine fishes are often associated with the freshwater environments of south-western Australia, while a number of others are occasionally encountered within freshwaters (Morgan *et al.* 1998). The Leschenault Inlet acts as a nursery ground for numerous fishes of marine origin, such as the mullets (Mugilidae) (Potter *et al.* 2000), but also supports

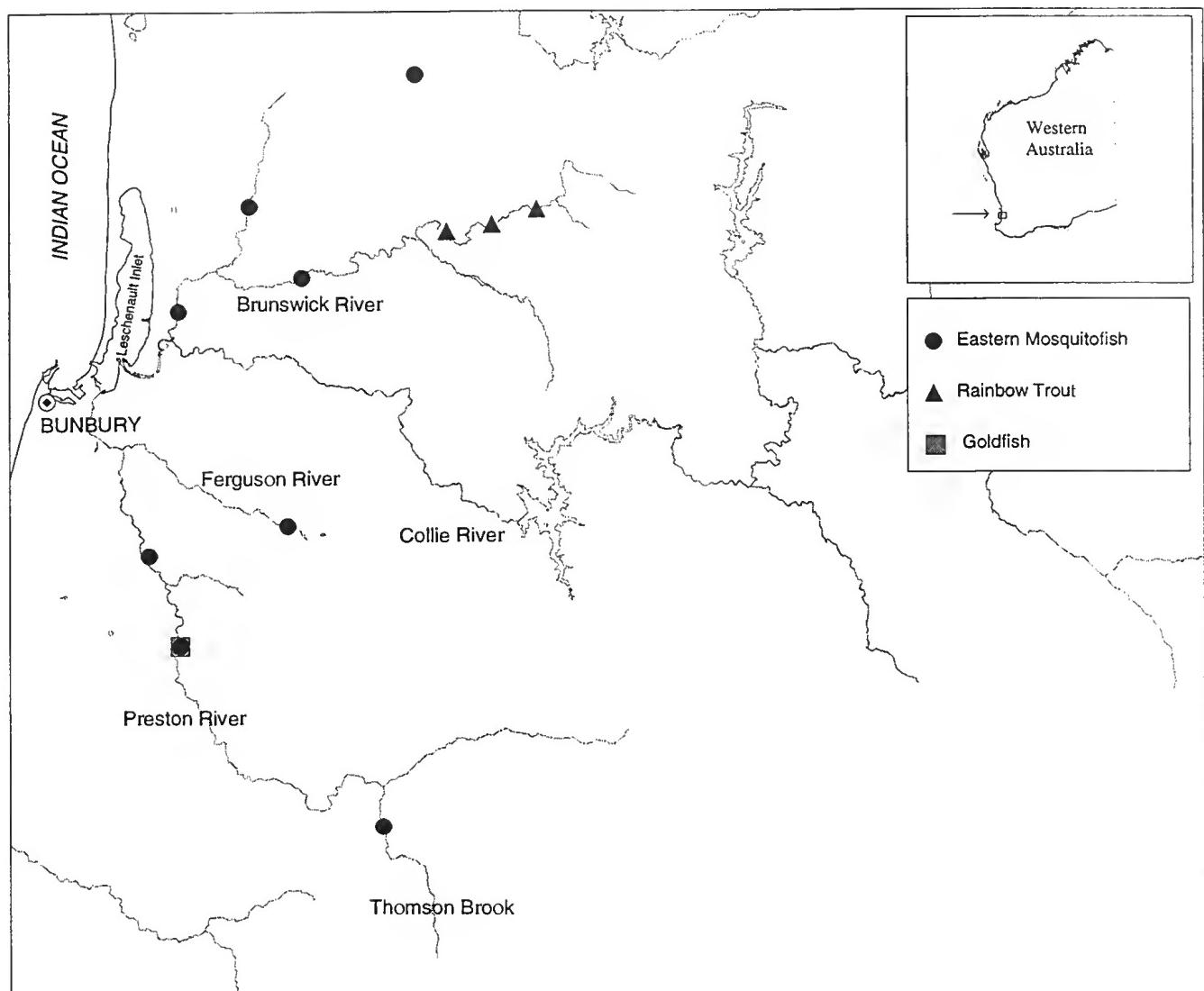


Figure 4. Capture locations of the introduced fishes in the Brunswick and Preston Rivers.

populations of a number of species that are termed estuarine. The typically estuarine Western Hardyhead, the Swan River Goby and the South-western Goby were found in both systems, however, only penetrated into the freshwater environments of the Preston River.

Each of these three species is commonly encountered within inland waters (rivers/lakes) of south-western Australia (Morgan *et al.* 1998). While it is not clear why these species do not move into the freshwaters of the Brunswick River, it is possible that either the channelised lower sections may not be conducive to these species or that the weir restricts their upstream movement.

The capture of a single Empire Gudgeon represents the first record of the species in the South-west Drainage Division. The capture of a single individual is surprising. It is possible that the individual may be an unwanted aquarium pet that entered the Preston River as the result of a deliberate release. However, it is also conceivable that it entered the system through the inlet from the marine environment as a larvae or juvenile from populations in the Pilbara (Indian Ocean) Drainage Division (see Morgan & Gill 2004). Gopurenko *et al.*

(2003) reported that larval drift from the north, via the Leeuwin Current, was the most likely factor accounting for the recent colonisation of south-western Australian estuaries by another tropical species, the Mud Crab (*Scylla serrata* (Forsskål, 1755)).

Some may argue that the Empire Gudgeon is strictly a freshwater species, but captures in north-western Australia strongly suggest that the species should be considered an estuarine species that moves into freshwater (see Morgan & Gill 2004) and it is known to sometimes be present in full strength sea water (Hoese & Allen 1983). The nearest populations of the species are in the Chapman and Murchison Rivers; possibly a result of larval drift from its more northerly locations in the Pilbara and Kimberley Drainage Divisions (Morgan & Gill 2004). Within the rivers of the Pilbara it is generally found in the lower reaches of rivers or in estuaries, e.g. Murchison River (Morgan & Gill 2004). Regardless of how the individual came to be in the Preston River, the capture of a single individual in the current study, suggests a larger self-maintaining population has not become established; however, a follow up survey is required to confirm this assumption.

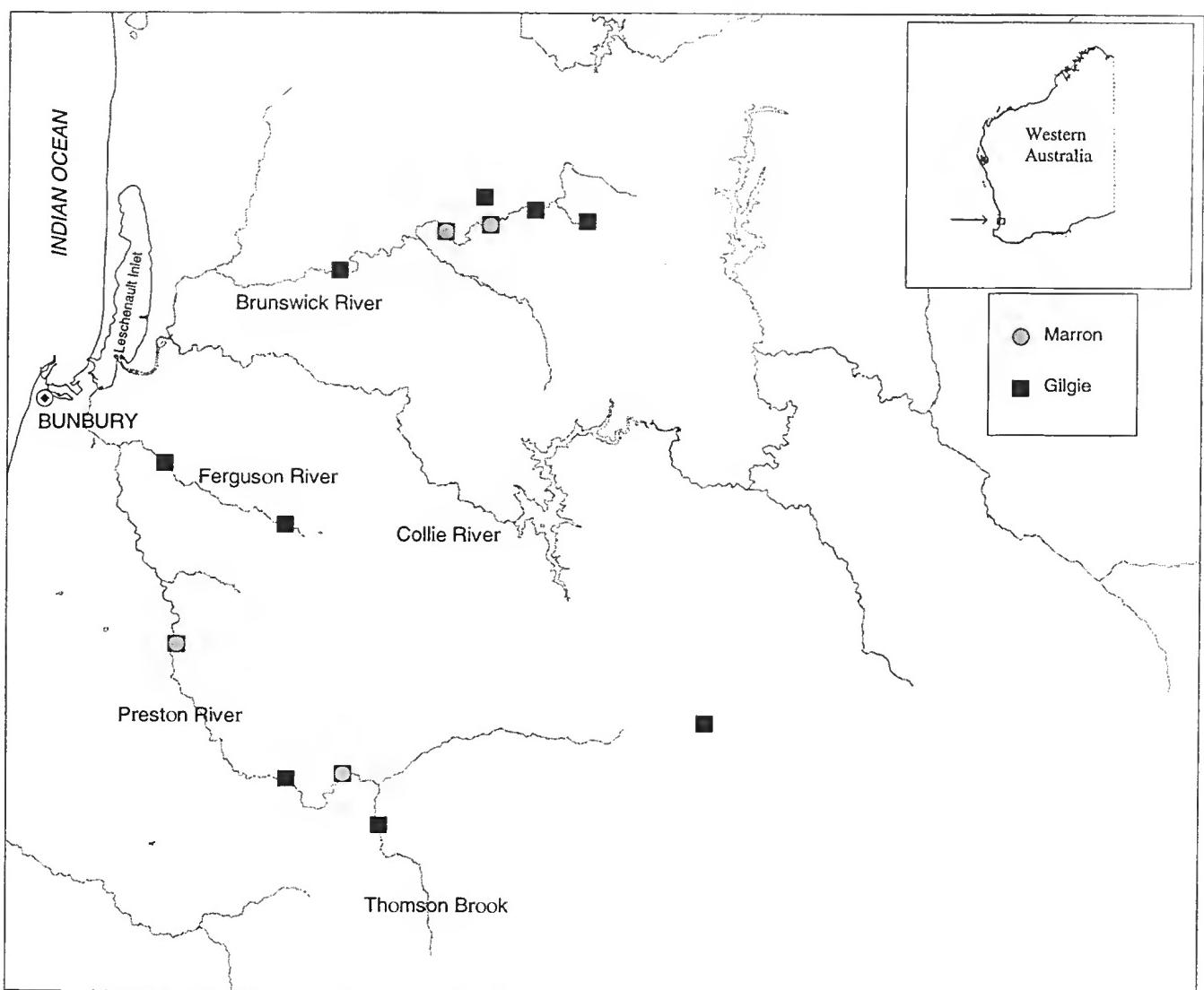


Figure 5. Capture locations of endemic freshwater crayfishes in the Preston and Brunswick Rivers.

A total of 10 species of introduced freshwater fish are reported from Western Australia (Morgan *et al.* 2004) with three of these (Goldfish, Rainbow Trout and Eastern Mosquitofish) being recorded during sampling in the current study. Other studies previously recorded Redfin Perch (*Perca fluviatilis* Linnaeus, 1758) in the Collie River (Morgan *et al.* 1998; Pen & Potter 1992).

As Goldfish were only found at site 10 below the weir on the Preston River (Figures 1 and 4), it is likely the barrier has limited their spread upstream. It may also suggest that the initial site of release was in the lower Preston River, potentially near the coastal urban centre of Bunbury (Fig. 1). Rainbow Trout were captured in the upper Brunswick River and these fish are most likely to have been fish that were stocked by the Department of Fisheries WA. Between 1999 and 2004 some 90000 Rainbow Trout fry were stocked into the Brunswick River, and a further 240000 fry and 8200 yearlings were stocked within the Collie River (Collie Gorge) during the same period. The impact of the continued stocking of trout into the Brunswick River should be assessed to determine predation levels on

native fish and freshwater crayfish. Impacts of Western Australia's introduced fishes are summarised in Morgan *et al.* (2004), and range from competition for food and habitat with native fishes to predation on native fishes and crayfishes.

## Conclusions

Perennial flows in the Brunswick and Preston Rivers support populations of a number of south-western Australia's endemic freshwater fishes, including the Western Minnow, Western Pygmy Perch, Nightfish, and Freshwater Cobbler. A number of typically estuarine fishes, including the Western Hardyhead, the Swan River Goby and the South-western Goby, were found within the freshwaters of the Preston River but none of these were found to penetrate into the freshwater environment of the Brunswick River. This study reported the Empire Gudgeon below the gauging station weir on the Preston River; the first record of it from the entire South-west Drainage Division. Its presence may have been due to either an aquarium release (either direct or is a progeny)

or larval drift from the Pilbara Drainage Division of Western Australia.

Two species of endemic freshwater crayfish, the Gilgigie and the Marron, were found within these systems. Both rivers are also occupied by the introduced Eastern Mosquitofish, while Goldfish were captured in the Preston River and Rainbow Trout were found within the Brunswick River; presumably as a consequence of a stocking programme in that system. Although some research has recently been conducted on the impacts of introduced fishes in the region (Morgan *et al.* 2004 and references therein), specific catchment based assessments should occur together with quantification of the impacts of instream barriers to, in particular, migratory patterns of the highly endemic fishes of this region.

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# Post-fire juvenile period of plants in south-west Australia forests and implications for fire management

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## Abstract

Regular prescribed burning to manage the accumulation of flammable live and dead vegetation (fuel) is a strategy for ameliorating wildfire impacts in fire-prone environments. The interval between prescribed fires needs to be sufficient to manage fuel accumulation but it should also be ecologically acceptable. Time to first flowering after fire (juvenile period) is a biological indicator that can be used to guide minimum intervals between fires to conserve plant diversity. A survey of 639 plant species in forests and associated ecosystems of south-west Western Australian revealed that 97% of understorey species reached flowering age within 3 years of fire and all species reached flowering age within 5 years of fire. Within species variation was evident, with plants at the drier end of their range taking longer to reach flowering age. Fire sensitive plants, being obligate seeder species with longer juvenile periods (> 3 years), mostly occurred in low rainfall zones so took longer to mature, or in habitats that were less prone to fire because they remained moist for a longer period or because surface fuels were inherently sparse and discontinuous. Due to uncertainty about the reproductive biology and seed bank dynamics of most of the flora, we recommend that the conservative minimum interval between fires that are lethal to fire sensitive plants is about twice the juvenile period of the slowest maturing species in the community. Occasional landscape fires at shorter intervals would be ecologically acceptable only if these fires were of a sufficiently low intensity as to not kill plants with long juvenile periods, or were patchy and did not burn the habitats in which they occur.

**Keywords:** fire, juvenile period, seeders, resprouters, prescribed burning

## Introduction

Plant communities in the south-west forest region of Western Australia display a remarkable array of physical and biological traits that enable them to persist in a fire prone environment, and in some cases depend upon fire for structural and floristic diversity (e.g., Gardner 1957, Christensen and Kimber 1975, Christensen and Abbott 1989 and Burrows and Wardell-Johnson 2003). Fire regime is the history of fire frequency, season and intensity (Gill 1981) with fire frequency affecting both the structure of the vegetation and its floristic composition (Muir 1987, Burrows and Wardell-Johnson 2003). Fire frequency also directly influences fire intensity because the quantity of live and dead vegetation, which becomes fuel for a bushfire, accumulates rapidly in the first 10 years after fire, after which the rate of fuel accumulation slows (Burrows 1994, McCaw *et al.* 1996).

Today, intense summer wildfires threaten human life, destroy property and damage forest values such as

timber and amenity. Large, intense wildfires can also be environmentally damaging and present a threat to ecosystem processes and conservation values including old growth forests, communities and species sensitive to high fire intensities, and extant populations of rare flora and fauna (see Abbott and Burrows 2003). Fire intensity, or the rate of heat energy release, is a measure of the severity of the fire; its damage potential, suppression difficulty and killing power. Wildfires derive their energy from the quantity and arrangement of live and dead vegetation (fuel) that burns. Fire intensity is further influenced by fuel dryness, weather conditions and topography. Of the factors that determine potential fire intensity, fuel quantity and weather conditions are the most influential, but fuel quantity is the only factor that can be effectively managed. Fuel reduction burning, the practise of purposefully setting low intensity fires under defined conditions of fuel, weather and topography, is a fire management technique to minimise the impact of wildfires by reducing the potential size and intensity of a wildfire, thereby reducing its damage potential and enhancing suppression opportunities. Prescribed burning does not prevent wildfires from occurring but where a significant proportion of the landscape is managed this

way, wildfire impact can be considerably reduced. While there are few published cases where this practice has effectively reduced the impact of wildfires and contributed to suppression success (e.g. Rodger 1961, Underwood *et al.* 1985, Grant and Wouters 1993), there are numerous unpublished accounts by firefighters and land managers where prescribed burning has ameliorated wildfires (Cheney 1994). However, the practice of prescribed burning for fuel reduction is controversial with concerns that it is ecologically damaging in the long term.

There have been many studies and observations of the ecological effects of a single fire on various plant species and communities in south-west ecosystems, however there are few published data on the long term ecological effects of repeated fuel reduction burning in south-west Australian forests (Christensen and Abbott 1989, Burrows and Wardell-Johnson 2003). Burrows and Wardell-Johnson (2003) reported that 30 years of very frequent burning (3–4 year intervals) of an experimental site in a southern jarrah (*Eucalyptus marginata*) forest did not result in any species losses, but caused changes in the relative abundance of species over time including a decline in the abundance of two obligate seeder species and an increase in abundance of several other species. They also reported that none of the experimental fire regimes favoured all species, including long periods of fire exclusion. There was evidence that burning at 5–7 year intervals in spring and autumn caused no significant changes to species richness or abundance at the study site.

In areas zoned for fuel reduction by prescribed burning, managers aim to maintain fine surface fuel quantity (dead leaves, twigs, bark and floral parts <6 mm in diameter) below about 8 t ha<sup>-1</sup> and 19 t ha<sup>-1</sup> for jarrah and karri (*E. diversicolor*) forests respectively. The higher fuel loading for karri reflects its more mesic, hence less flammable condition for a longer period throughout the year (McCaw and Hanstrum 2003). The time taken for fuels to reach these levels, hence the interval between prescribed fires, depends on the rate of fuel accumulation. This varies across the forest region from about 6 to 10 years, depending on site productivity and rainfall (Sneeuwagt and Peet 1985, Burrows 1994). For example, in most jarrah forests, fine surface fuel quantity reaches quasi-equilibrium in 15–17 years (Burrows 1994).

While about 70% of jarrah forest plant species have the capacity to resprout following fire, the remainder depend on seed (obligate seeders), stored either in the soil (soil-stored seeders) or in woody capsules in the canopy (canopy-stored seeders), for regeneration (Christensen and Kimber 1975, Burrows and Wardell-Johnson 2003). An adequate viable seed store and conditions favourable for seed germination and plant growth are essential for flowering plants to persist in an ecosystem that is regularly burnt. For some species, fruit production and seed set may not occur in the first flowering year (Benson 1985, Wark *et al.* 1987, Burrows and Wardell-Johnson 2003) and seed production sufficient to provide adequate seed reserves to restore the population to pre-fire abundance levels may take many years (Gill and McMahon 1986, Gill and Nicholls 1989, Wooller *et al.* 2002). As observed by Gill and Nicholls (1989), seed production is the most relevant

measure but flowering is a more practical measure. Gill and Nicholls (1989) suggest that doubling of the juvenile period of a species is a useful guide to when the species is likely to be able to replenish its seed bank following fire. This 'rule of thumb' is consistent with a number of individual species studies of seed production with time (see review by Burrows and Wardell-Johnson 2003). However, there is a paucity of information about the reproductive biology and seed bank dynamics of plant species in Australian ecosystems (Whelan 1995, Burrows and Wardell-Johnson 2003). Until more is known, knowing the juvenile period of species in an ecosystem subjected to regular fire is a useful criterion for determining the minimum fire interval between lethal fires and for assisting with defining ecologically sustainable fire regimes (Tolhurst 1999, Tolhurst 2004). If the interval between fires that are lethal to the parent plants is shorter than the time to first flowering (juvenile period) and seed set, then it is reasonable to assume that obligate seeder species especially, could be at risk of decline. However, if the intensity or patchiness of fires at short intervals is such that parent plants are not killed by fire, then populations may be able to persist and thrive under a regime of frequent but very low intensity, patchy fires.

This paper reports on post-fire regeneration strategies, post-fire juvenile period and flowering phenology of 639 species that occur predominantly in the southern forests and associated ecosystems of south-west Western Australia. We also discuss how other factors such as climate (rainfall), regeneration strategy and life form influence age to first flowering.

## Methods

### Study sites

Information about post-fire regeneration strategies, flowering time (month) and juvenile period (months) was gathered from study sites in the southern forest region of the south-west of Western Australia (Fig. 1). A brief description of each site is given in Table 1. The McCorkhill and Yendicup forest sites each comprised 10 small (each 4 ha) adjacent plots that were experimentally burnt at various times as part of a broader investigation into the long term effects of fire (see Burrows and Wardell-Johnson 2003). The Lindsay forest site (Table 1) was similar except the plots were smaller (each about 0.5 ha). Data from the Walpole study site (Table 1) were accumulated from some 400 vegetation sample sites located throughout a broad range of vegetation types represented in the Walpole-Nornalup National Park (see Wardell-Johnson *et al.* 1989). Post-fire regeneration strategy and juvenile period were assessed at each site by regular (3–4 weekly) inspections until all species at the site had reached flowering age. The juvenile period is quite variable amongst individuals of the same species in the same population, so we define juvenile period as the time taken for at least 50% of individuals in a population to reach flowering age after fire. This was assessed visually. Visual inspection also ascertained the post-fire regeneration strategy, and plants were classified as shown in Table 2, which has been adapted from Gill (1981). Some species regenerated by more than one of the

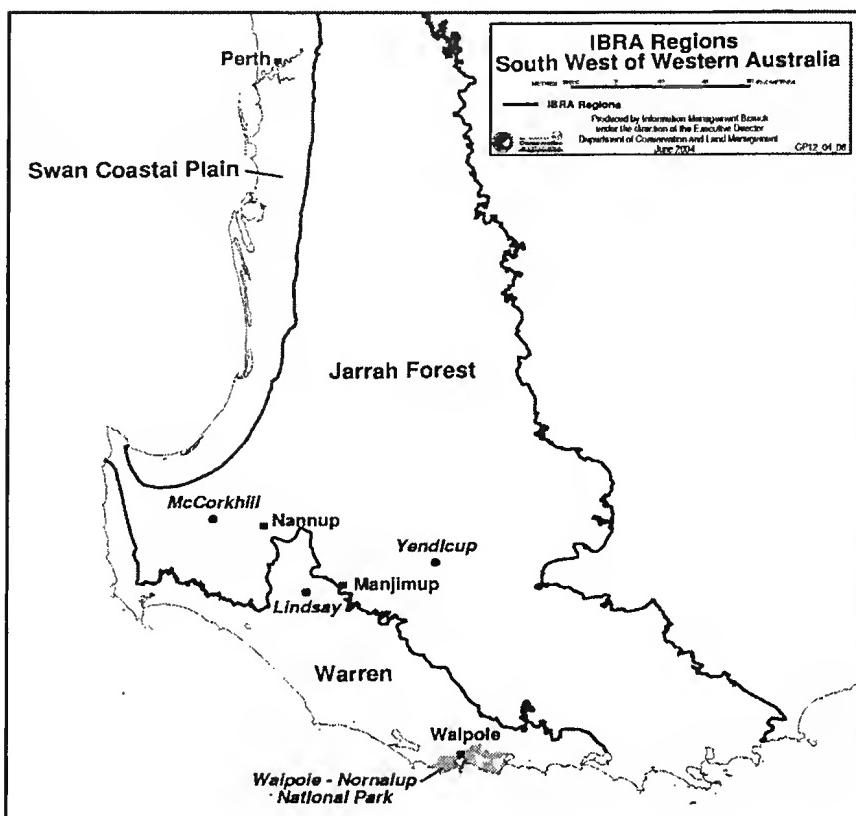


Figure 1. Location of survey sites at McCorkhill forest, Lindsay forest, Yendicup forest and the Walpole-Nornalup National Park in south-west Western Australia from which information about the post-fire juvenile period, regeneration strategy and time of flowering of 639 plant species was gathered.

Table 1

Location and general description of vegetation, soils, landform and climate of sites in south-west Australia forest and associated ecosystems surveyed for post-fire regeneration and flowering responses.

Location	General description of vegetation	Soils and landform	Climate
McCorkhill forest: 20 km west of the town of Nannup. Latitude 33° 57.4' S, Longitude 115° 32.5' E	Havel and Mattiske (2000) vegetation complex type 'Kingia'. Open forest, overstorey dominated by <i>Eucalyptus marginata</i> and <i>Corymbia calophylla</i> 20–25 m tall. Second storey of <i>Allocasuarina fraseriana</i> , <i>Banksia grandis</i> and <i>Persoonia longifolia</i> to 6 m tall. Low woody shrub and herb understorey to 1 m tall.	Yellow brown gravelly sands on ridges and undulating slopes.	Mediterranean-type climate with cool wet winters and warm dry summers. Mean annual rainfall 1 000 mm.
Lindsay forest: 12 km west of the town of Manjimup. Latitude 34° 14.6' S, longitude 115° 58.0' E.	Havel and Mattiske (2000) vegetation complex type 'Crowea'. Tall open forest of <i>C. calophylla</i> and <i>E. marginata</i> with some <i>E. diversicolor</i> 30–35 m tall. Second storey of <i>Xylonielum occidentale</i> , <i>B. grandis</i> and <i>P. longifolia</i> to 6 m tall. Woody shrub and herb understorey to 1.5 m tall.	Yellow duplex soils with pale brown sandy loam topsoil on ridges and midslopes.	Mediterranean-type with cool wet winters and warm dry summers. Mean annual rainfall 1 150 mm.
Yendicup forest: 45 km west of the town of Manjimup. Latitude 34° 11.6' S, longitude 116° 37.0' E.	Havel and Mattiske (2000) vegetation complex type 'Frankland Hills'. Woodland of <i>E. marginata</i> and <i>C. calophylla</i> 15–20 m tall. No significant second storey. Open woody shrub and herb understorey to 0.5 m tall.	Yellow brown gravelly duplex soils with some laterite boulders.	Mediterranean-type with cool wet winters and warm dry summers. Mean annual rainfall 750 mm.
Walpole-Nornalup National Park: 18 390 ha on the south coast of Western Australia. Surrounds the town of Walpole	Wardell-Johson et al. (1989) described 15 vegetation communities including a variety of heathlands, woodlands, low open eucalypt forests and tall eucalypt forests.	Diversity of soils and landforms. See Wardell-Johson et al. (1989) and CALM (1990).	Mediterranean type climate with cool wet winters and mild summers. Mean annual rainfall varies across the Park from 1 200–1 300 mm.

Table 2

Classification of post-fire regeneration strategies of vascular plants in south-west Australia ecosystems (adapted from Gill 1981).

Seeders	Resprouters
(1) Stem girdling or 100% scorch kills, depends on canopy stored seed	(4) Survives stem girdling or 100% scorch, soil suckers (rhizome, corm, bulb, tuber)
(2) Stem girdling or 100 % scorch kills, depends on soil stored seed	(5) Survives stem girdling or 100% scorch, basal sprouts (lignotuber)
(3) Stem girdling or 100% scorch kills, no stored seed	(6) Survives 100% scorch, epicormic shoots
(8) Stem girdling or 100% scorch kills, any of 1,2,3 above	(7) Survives 100% scorch, large apical bud
(10) Ferns and Allies (spores)	(9) Survives 100% scorch, any of 4,5,6,7 above

categories shown above. For example some lower tree and overstorey tree species in particular, including *Banksia grandis* and *Eucalyptus marginata*, were capable of resprouting from either a subterranean lignotuber or epicormic buds, or of regenerating from seed, depending on the fire intensity and the physiological age of the plant (Burrows 1985). In these cases, species were deemed to be resprouters and allocated to one of the resprouter categories shown in Table 2. Some thin barked tall shrub species that are typically characterised as obligate seeders, such as *Melaleuca viminea*, have occasionally been observed to resprout following very low intensity fire which scorched the canopy but did not girdle the main stem. Such species were classified as obligate seeders in this study.

## Results

Information on post-fire regeneration strategy, juvenile period and peak flowering month was

documented for 639 plant species representing 249 genera and 72 families (Table 3). The most commonly observed families were Orchidaceae, Proteaceae, Papilionaceae, Myrtaceae, Epacridaceae, Asteraceae and Mimosaceae. The least commonly observed families included Portulaceae, Cephalotaceae, Lindsaeaceae, Zamiaceae, Loranthaceae, Podocarpaceae and Dennstaedtiaceae. At the intermediate and high rainfall sites (McCorkhill forest near Nannup, Lindsay forest near Manjimup and Walpole-Nornalup National Park), all upland forest understorey species reached flowering age within 3 years of fire, with most (90%) flowering within 2 years (Fig. 2). At the lower rainfall site (Yendicup forest near Perup) all upland forest understorey species reached flowering age within 4 years of fire. Of the 639 species observed, 17 (3%) species had juvenile periods >3 years and three species were observed to take longer than 4 years to reach flowering after fire. These were *Banksia brownii* (5 yrs), *B. seminuda* (5 yrs) and *Melaleuca viminea* (5 yrs) (Table 4). Species with longer juvenile periods were mostly

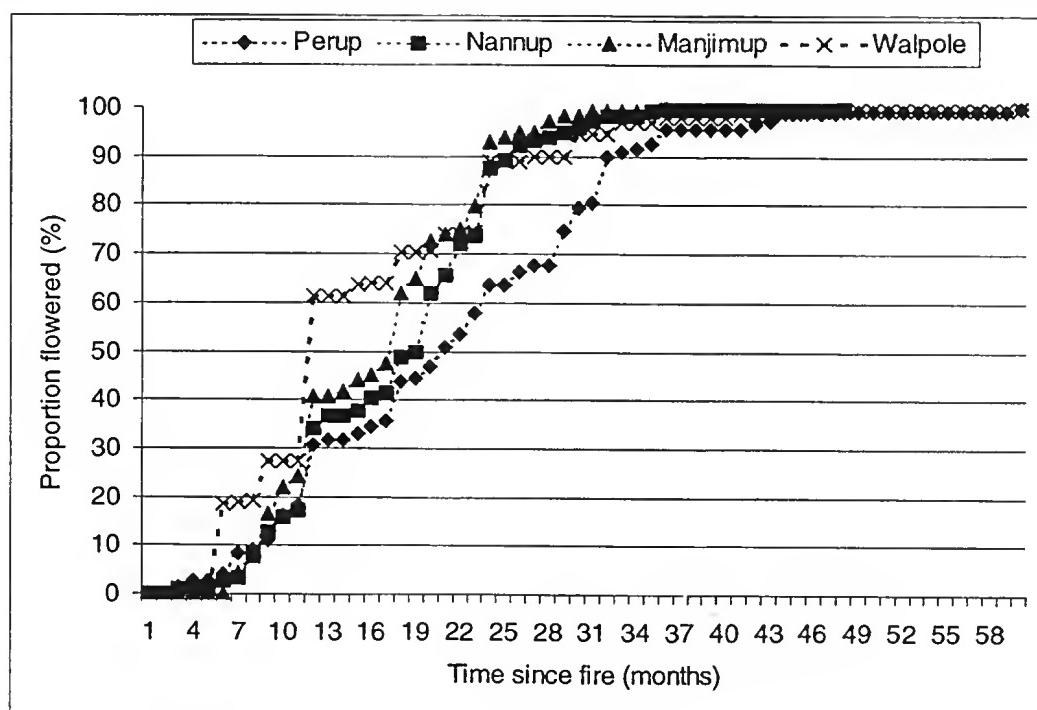


Figure 2. Cumulative proportion of species to have reached flowering age with time since fire for 639 species from four locations in the south-west forest region of Western Australia. A species was deemed to have reached flowering age when at least 50% of the population had flowered.

**Table 3**

Plant families surveyed ranked by number of species in each family

Family	No. Genera	No. Species
Orchidaceae	20	76
Proteaceae	19	64
Papiliopteraceae	18	59
Myrtaceae	17	46
Epacridaceae	9	28
Asteraceae	18	28
Mimosaceae	2	27
Poaceae	15	23
Styliadiaceae	2	23
Goodeniaceae	6	20
Cyperaceae	9	16
Apiaceae	9	16
Dilleniaceae	1	16
Dasygordonaceae	5	15
Anthericaceae	8	15
Rutaceae	5	13
Thymelaeaceae	1	9
Haemodoraceae	3	9
Droseraceae	1	8
Restionaceae	6	8
Sterculiaceae	3	6
Lobeliaceae	1	6
Tremandraceae	3	6
Iridaceae	2	6
Colchicaceae	2	6
Polygalaceae	2	5
Lamiaceae	2	5
Santalaceae	3	4
Haemodoraceae	1	4
Euphorbiaceae	4	4
Loganiaceae	2	4
Rubiaceae	1	3
Pittosporaceae	2	3
Rhamnaceae	2	3
Casuarinaceae	1	3
Lentibulariaceae	1	3
Haloragaceae	2	2
Stackhousiaceae	2	2
Xanthorrhoeaceae	2	2
Lauraceae	1	2
Ranunculaceae	2	2
Phormiaceae	2	2
Geraniaceae	2	2
Scrophulariaceae	2	2
Solanaceae	1	2
Campanulaceae	1	2
Hypoxidaceae	1	2
Onagraceae	1	2
Amarathaceae	1	2
Caesalpiniaceae	1	1
Gyrostemonaceae	1	1
Violaceae	1	1
Phormiaceae	1	1
Centrolepidaceae	1	1
Aspleniaceae	1	1
Linaceae	1	1
Malvaceae	1	1
Brassicaceae	1	1
Primulaceae	1	1
Olacaceae	1	1
Saxifragaceae	1	1
Byblidaceae	1	1
Maryanthaceae	1	1
Sapindaceae	1	1
Xyridaceae	1	1
Portulaceae	1	1
Cephalotaceae	1	1
Lindsaeaceae	1	1
Zamiaceae	1	1
Loranthaceae	1	1
Podocarpaceae	1	1
Dennstaedtiaceae	1	1
<b>Total: 72</b>	<b>249</b>	<b>639</b>

canopy-stored seeders that occurred in less flammable habitats such as moist parts of the landscape (e.g., riparian zones, some swamps) or where surface fuels were discontinuous or sparse (e.g., rock outcrops, some swamps) (Table 4).

Intra-species variation in juvenile period was evident locally and regionally with plants growing in the lower rainfall areas often taking considerably longer to flower than the same species at higher rainfall sites. Some examples are shown in Table 5.

Mean juvenile period, or secondary juvenile period in the case of resprouters (Gill 1975), for various plant life forms is shown in Table 6. As to be expected, trees, lower trees and woody shrubs took longer to flower after fire than geophytes, grasses and annual herbs. All overstorey tree species (*Eucalyptus* spp.) and many lower tree species (e.g. some *Banksia* spp.) were capable of both resprouting and regenerating from seed after fire; the juvenile period reported here is for mature plants that have re-sprouted. The juvenile period of plants regenerating from seed would be considerably longer (probably 10–20 years for eucalypts). There was a statistically significant difference ( $\alpha = 0.05$ ) in juvenile period between seeders and resprouters in almost all life form categories with resprouters flowering sooner than obligate seeders, the exception being grasses, where seeders flowered sooner. Mean juvenile period for plants in each of the nine post-fire regeneration categories is shown in Figure 3. Overall, canopy-stored seeders had the longest juvenile period (mean about 36 months) and geophytes (especially Orchidaceae, Droseraceae) and plants with large apical buds (Xanthorrhoeaceae and Dasygordonaceae) took the shortest time to flower (mean about 10 months). *Kingia australis* (Dasygordonaceae) had the shortest juvenile period with most of the population flowering within 2 months of fire; plants with stems shorter than about 100 cm had few or no flowers, suggesting they had not reached reproductive maturity.

While flowering occurred throughout the year, there is a distinctive flowering peak during spring when about 60% of plants flower. Few plants flowered during the

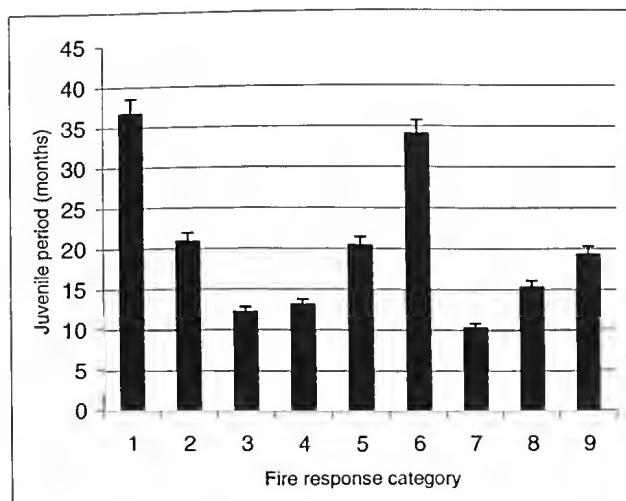


Figure 3. The mean juvenile period for plant species categorised according to post-fire regeneration response strategy. Fire response categories are shown in Table 2.

Table 4

Shrubs and small trees species with known juvenile periods > 3 years. Habitat flammability rating takes account of seasonal moisture regime and fuel characteristics including quantity, structure and continuity.

Species	Conservation Status	Post-fire regeneration strategy	Juvenile period (months)	Distribution and Habitat	Habitat Flammability Rating
<i>Acacia pentadenia</i> Lindl.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	36 (Pemberton) 48 (Walpole-Nornalup NP)	Southern jarrah and karri forests and coastal areas. Loamy soils, moist and swampy areas.	LOW: High fuel accumulation rate but fuel complex stays moist for long periods of the year. Note: Juvenile period variable across range, depending on site productivity.
<i>Banksia brownii</i> R.Br.	Declared rare	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Walpole-Nornalup NP)	Restricted distribution, Walpole-Nornalup NP-Albany. Rock outcrops, gullies. Throughout the lower south-west, Busselton to Katanning. Swamp margins, seasonally wet flats.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry windy conditions for fire spread.
<i>Banksia meisneri</i> Lehm.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (McCorkhill forest)	South coast and adjacent hinterland, Augusta to Esperance. Low lying areas, swamps, seepages, consolidated sand dunes.	MODERATE: Fuel complex stays moist for longer period, low sparse surface fuels, often dense elevated heath fuels requiring wind for spread.
<i>Banksia occidentalis</i> R.Br.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (McCorkhill forest) 36 (Walpole-Nornalup NP)	South coast and adjacent hinterland, Pemberton to Albany. Swamps, seasonally wet flats.	MODERATE: Fuel complex stays moist for longer period. Usually burns under drier summer/autumn conditions.
<i>Banksia quercifolia</i> R.Br.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (Walpole-Nornalup NP)	South coast and adjacent hinterland, Pemberton to Albany. Swamps, seasonally wet flats.	MODERATE: Fuel complex stays moist for longer period, low sparse surface fuels, often dense elevated heath fuels requiring wind for spread.
<i>Banksia seminuda</i> (A.S. George) Rye	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Walpole-Nornalup NP)	Throughout lower south-west, Dwellingup to Albany. Riverine, consolidated dunes, rock outcrops.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/autumn conditions.
<i>Banksia verticillata</i> R.Br.	Declared rare	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (Walpole-Nornalup NP)	South coast, Walpole-Nornalup NP to Albany. Rock outcrops.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry, windy conditions for fire spread.
<i>Calothamnus rupestris</i> Schauer	Priority four	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Northern jarrah forest)	Rock outcrops in the northern jarrah forest.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry, windy conditions for fire spread.
<i>Dryandra lindleyana</i> Meisn.	Not threatened	Survives stem girdling or 100% scorch, soil suckers (rhizome, corm, bulb, tuber)	42 (Yendicup forest) 32 (McCorkhill forest)	Widespread throughout south-west, Geraldton to Albany. Habitat variable across range.	HIGH: Commonly occurs in midslope and upland jarrah forests and woodlands with continuous cover of surface fuel. Note: Juvenile period variable across range, depending on site productivity.

<i>Grevillea occidentalis</i> R.Br.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	44 (Yendicup forest)	Lower south-west and south coast, Walpole- Nornalup NP to Albany. Sand over laterite or granite, loam, gravel.	LOW-MODERATE: Commonly occurs in jarrah woodlands and swamp margins. Low fuel accumulation rates.
<i>Hovea trisperma</i> Benth.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	42 (Yendicup forest) 22 (McCorkhill forest)	Widely distributed throughout south-west forests and south coast. Variety of habitats across range.	Occurs in a wide range of fuel complexes. Note: juvenile period variable across range, depending on site productivity.
<i>Lambertia orbifolia</i> C.A.Gardner	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	40 (Scott River)	Restricted distribution, coastal areas- Busselton, Margaret River, Albany. Creeksides, dunes, swamps.	LOW: Coastal heaths, swamps, wet areas. Requires dry, windy conditions for fire spread.
<i>Lambertia rariflora</i> Meisn. subsp. <i>jutea</i> Hnatuk	Priority three	Stem girdling or 100% scorch kills, depends on soil-stored seed	48 (Walpole- Nornalup NP)	Restricted distribution Walpole- Nornalup NP region. Creeksides, seasonally wet areas, occasionally mid-slopes and ridges.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions.
<i>Lambertia rariflora</i> Meisn. subsp. <i>rariflora</i>	Priority four	Stem girdling or 100% scorch kills, depends on soil-stored seed	48 (Margaret River)	Restricted distribution Busselton- Margaret River area. Creeksides.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions.
<i>Lasiopteratum floribunda</i> Benth.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	44 (Yendicup forest) (24 Lindsay forest)	Widespread throughout forest region	Occurs in a wide range of fuel complexes. Note: juvenile period variable across range, depending on site productivity.
<i>Leucopogon pulchellus</i> Sond.	Not threatened	Stem girdling or 100% scorch kills, depends on soil-stored seed	43 (Yendicup forest) 30 (McCorkhill forest)	Northern and central jarrah forests. Mainly lateritic or granitic soils.	HIGH: Occurs in tall forest and woodland fuel complexes. Note: juvenile period variable across range, depending on site productivity.
<i>Melaleuca thymoides</i> Labill.	Not threatened	Survives stem girdling and 100% scorch, basal sprouts (lignotuber)	44 (Yendicup forest) 20 (McCorkhill forest)	Widespread throughout south-west forests and great southern, Perth to Esperance. Winter wet depressions, granite hills, sand dunes.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions. Note: juvenile period variable across range, depending on site productivity.
<i>Melaleuca viminea</i> Lindl.	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	60 (Yendicup forest)	Widespread throughout the south-west from Geraldton to Esperance. Creeksides, winter wet depressions, rocky coastal areas, flats.	LOW: Often low, sparse and patchy surface fuel accumulation. Requires dry, windy conditions for fire spread.
<i>Taxandria juniperina</i> (Schauer) J.R.Wheeler & N.G.Marchant	Not threatened	Stem girdling or 100% scorch kills, depends on canopy-stored seed	48 (Pemberton)	South coast and adjacent hinterland from Busselton to Albany. Watercourses and swamps.	LOW-MODERATE: Fuel complex stays moist for longer period. Usually only burns under drier summer/ autumn conditions.

**Table 5**

Examples of intra-species variation in juvenile period (months) with variation in mean annual rainfall

Species	Low rainfall (750 mm annum <sup>-1</sup> )	High and intermediate rainfall (1 000–1 350 mm annum <sup>-1</sup> )
<i>Agrostocrinum scabrum</i> (R.Br.) Baillon	20	12
<i>Allocasuarina humilis</i> (Otto & F.Dietr.) L.A.S.Johnson	35	24
<i>Astrolooma drummondii</i> Sonder	24	12
<i>Billardiera variifolia</i> DC.	26	12
<i>Bossiaea linophylla</i> R.Br.	36	24
<i>Clematis pubescens</i> Endl.	32	18
<i>Conospermum caeruleum</i> R.Br.	32	12
<i>Daviesia preissii</i> Meisn.	30	12
<i>Gompholobium torrentosum</i> Labill	31	20
<i>Hakea amplexicaulis</i> R.Br	30	18
<i>Hibbertia rhadinopoda</i> F.Muell.	21	12
<i>Lasiopetalum floribunda</i> Benth	44	24
<i>Melaleuca thymoides</i> Labill.	44	24
<i>Petrophile diversifolia</i> R.Br.	36	26
<i>Velleia trinervis</i> Labill.	32	20

**Table 6**

Mean time (months) to first flowering after fire (juvenile period) for various life form categories and by primary post-fire regeneration strategy. Standard errors in parentheses.

Life form	Regeneration strategy
Tree or lower tree	Seeders
Woody shrub	36.9 (2.0)
Perennial herb	24.8 (0.7)
Short-lived herb	15.0 (1.0)
Grass	14.5 (0.7)
Sedge	11.3 (0.8)
Geophyte	None observed
	None observed
	10.3 (0.3)

late autumn and winter months (Fig. 4). The number of plant species in each of the post-fire regeneration categories and for three broad rainfall zones is shown in Table 7. Overall, about 70% of plants resprouted following fire and about 30% regenerated from seed. Only 1–2% of species relied on seed stored in the canopy (canopy-stored seeders) whereas 25–30% relied on seed stored in the soil (soil-stored seeders).

## Discussion

An ability to flower and to produce viable seeds in inter-fire periods is fundamental to the persistence of vascular plants in fire-prone environments, especially those that depend on seed stored on the plant (canopy-

**Table 7**

The number and proportion (%) of species in each post-fire response category for three rainfall zones of the south-west forests and associated ecosystems.

Post-fire regeneration strategy	McCorkhill forest Low rainfall (~750 mm annum <sup>-1</sup> )	Yendicup forest Intermediate rainfall (~1 000 mm annum <sup>-1</sup> )	Lindsay forest and Walpole-Nornalup National Park High rainfall (~1 150–1 350 mm annum <sup>-1</sup> )
1. Stem girdling or 100% scorch kills; canopy stored seed	3 (1.7%)	4 (1.5%)	5 (1.3%)
2. Stem girdling or 100% scorch kills; soil stored seed	46 (26.6%)	69 (25.6%)	114 (30.2%)
3. Stem girdling or 100% scorch kills; no stored seed	0 (0%)	1 (0.3%)	3 (0.8%)
4. Survives stem girdling or 100% scorch; soil suckers (rhizome, corm, bulb, tuber)	52 (30.2%)	69 (25.6%)	133 (35.3%)
5. Survives stem girdling or 100% scorch; basal sprouts (lignotuber)	60 (34.7%)	99 (36.6%)	79 (20.2%)
6. Survives 100% scorch; epicormic shoots	3 (1.7%)	15 (5.5%)	14 (3.7%)
7. Survives 100% scorch; large apical bud	2 (1.2%)	5 (1.8%)	3 (0.8%)
8. Stem girdling or 100% scorch kills; any of 1,2,3 above	6 (3.4%)	5 (1.8%)	21 (5.6%)
9. Survives 100% scorch, any of 4,5,6,7	1 (0.5%)	2 (0.6%)	3 (0.8%)
10. Ferns and Allies (spores)	0 (0%)	1 (0.3%)	2 (0.5%)
Total	173 (100%)	270 (100%)	377 (100%)

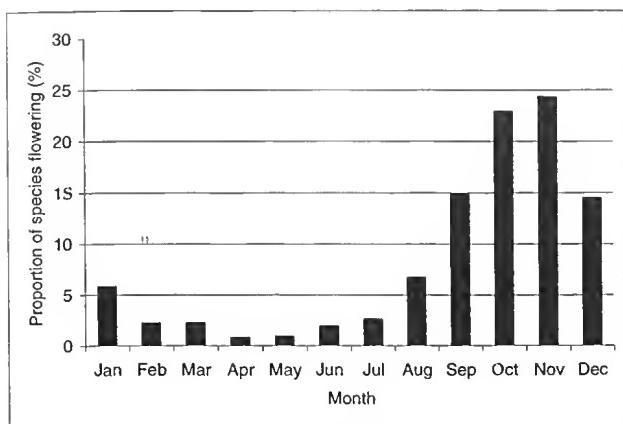


Figure 4. Proportion of species flowering in each month of the year.

stored seeders). While these species make up only 1–2% of all species observed (Table 6), they are often threatened taxa, have a limited distribution or are thicket forming, keystone species providing important habitat for other organisms. Of the 639 species observed in this study, 619 (~97%) reached flowering age within three years of fire, and all species had flowered within 5 years of fire. While this sample (639) is about a quarter of the known flora of the region, it represents a cross-section of habitat types, life forms and of taxa. This relatively rapid post-fire growth and maturation (short juvenile period) is not surprising given these ecosystems have a very long association with fire. Understorey species with juvenile periods longer than 3 years were confined to either the less productive lower rainfall zones of the forest region or to less flammable habitat elements in the landscape. The importance of climate (especially rainfall) in influencing juvenile period is further evidenced by the intra-specific variation shown in Table 5. Habitat flammability is broadly determined by the seasonal rhythm of moisture regime (McCaw and Hanstrum 2003) or by the quantity, structure and continuity of the vegetation complex, which becomes fuel for a bushfire. Parts of the landscape that stay moist for longer periods, such as some riparian zones, valley floors and swamp complexes, have a shorter period of the year when live and dead vegetation (fuel) is sufficiently dry to sustain fire, therefore a lower probability of combusting, so it is not surprising that species with longer juvenile periods most often occur in these areas. Other flat or low-lying, moisture gaining parts of the landscape, such as some myrtaceous swamps, are highly flammable for long periods of the year because of greater exposure to wind and solar radiation and because of the nature, structure and quantity of the elevated vegetation. However, it is unusual to find species with long juvenile periods in these habitats. Habitats with low or discontinuous fuels (such as rock outcrops and some swamp and woodland complexes) usually only carry fire under dry and windy conditions, further limiting the time throughout the year when conditions are such that these areas can burn. Thus, and as to be expected, understorey species with longer juvenile periods (>3 years) occur in habitats that are less prone to fire and are commonly tall shrubs and lower tree species such as *Banksia* spp. (Table 4). On the

other hand, plants with long juvenile periods are rarely found in parts of the landscape that are more prone to fire because these habitats are drier for longer periods and support continuous surface fuels, such as forested plateaus and uplands (see Table 4). Clarke (2002) working in south-east Australian forest ecosystems reported that rock outcrops and pavements were dissimilar in species composition from the surrounding forest and were dominated by shrubs that were readily killed by fire and depended on post-fire seedling recruitment. In contrast, the most abundant species in the adjacent, more flammable forest, were post-fire resprouters.

Muir (1987) found that of the 198 plant species he observed throughout the south-west, mid-west, wheatbelt, south coast and goldfields regions of Western Australia, almost 74% flowered within 4 years of fire, but about 26% took 5–8 years to flower. Of the species that took 5–8 years to flower, 7 (13%) occurred in the forest region, the remainder occurring in the lower rainfall areas outside the forest region. Of these, four are resprouters (*Agonis flexuosa*, *Astartea fascicularis*, *Banksia grandis* and *Regelia ciliata*), which we recorded flowering 24–36 months after fire, and the remainder (*Casuarina obesa*, *Melaleuca diosmifolia* and *M. laterita*) occur in or around swamps or winter-wet depressions. Van der Moezel et al. (1987) documented the juvenile period of 192 species of the northern sandplain kwongan near Badgingarra (mean annual rainfall about 500 mm) and reported that 79% of species flowered within 2 years of fire, with all species observed flowering within 5 years of fire. These data support the proposition that mean annual rainfall and spatial and temporal variability in landscape flammability are significant factors influencing the distribution of fire regime sensitive plant species, which are mostly obligate seeder species with relatively long juvenile periods.

Fine surface fuel (dead leaves, twigs, bark, fruits) on the forest floor provides the dominant fuel layer because of its position (at the base of the fuel ladder), quantity and continuity (Burrows 1994). Forest fires are unlikely to spread when the surface fuel moisture content exceeds about 21% or when the surface fuel quantity is below about 4 t ha<sup>-1</sup> (Burrows 1994). Under extreme fire weather conditions, which are likely to occur on only 1–2 days each year (McCaw and Hanstrum 2003), fire spread may be sustained when the surface fuel quantity is as low as 3 t ha<sup>-1</sup> but fires are generally low intensity and patchy. Surface fuels in upland jarrah forests re-accumulate to 4 t ha<sup>-1</sup> in about 2.5–4 years, depending on the structure and productivity of the forest (Fig. 5). From Figure 5, it can be seen that the shortest time after fire that jarrah forests will re-burn (2.5–4 yrs) is similar to the juvenile period of the slowest maturing understorey plants (3–4 years) shown in Figure 2. This is unlikely to be coincidence; it is likely that plants with longer juvenile periods, particularly obligate seeders, have been unable to persist in habitats that have the potential to re-burn at 3–4 year intervals. In the forest region, plants with longer juvenile periods are confined to habitats that have a lower probability of burning because of favourable moisture regimes or because of the discontinuous structure of the fuel complex, as discussed above.

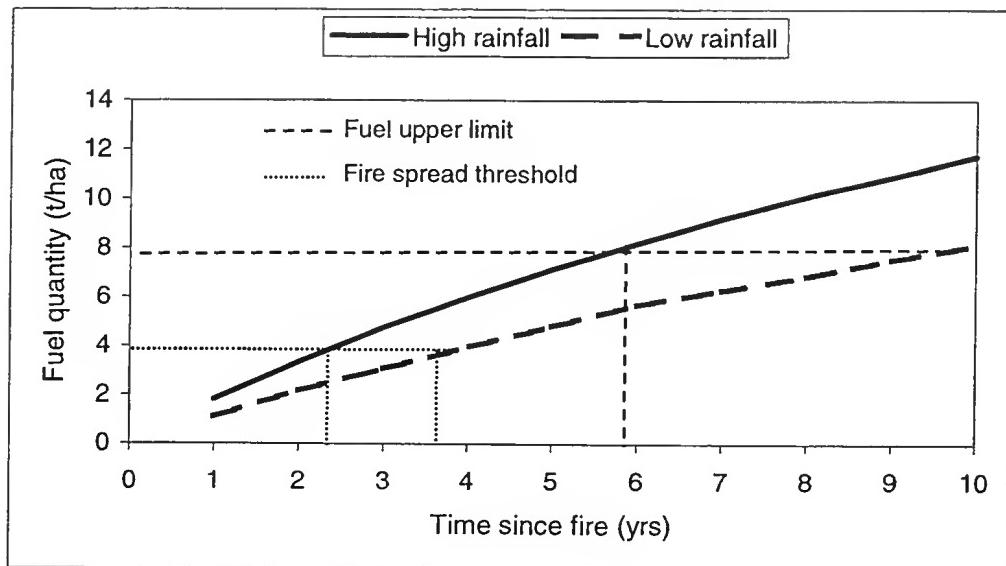


Figure 5. Fine surface fuel accumulation rates for high rainfall (Lindsay forest) and low rainfall (Yendicup forest) jarrah forests. The fuel upper limit is the quantity below which fuels are maintained by prescribed burning in strategic areas to assist wildfire control. The fire spread threshold is the fuel quantity below which fire spread is unlikely.

#### Management implications

Prescribed burning for fuel management in jarrah forests aims to maintain fine surface fuel quantities in strategic areas below about  $8 \text{ t ha}^{-1}$  (McCaw and Burrows 1989). Knowledge of fire behaviour and operational experience has shown that fires burning in heavier fuels and under warm, dry and windy conditions in summer are difficult, dangerous or impossible to control (Underwood *et al.* 1985), cause considerable physical damage to forest ecosystems (Peet and Williamson 1968 and Burrows 1987) and generally burn most of the landscape, leaving few if any, unburnt patches. The time taken for fine surface fuels to re-accumulate to  $8 \text{ t ha}^{-1}$  varies depending on the structure and productivity of the forest, which is largely dependent on annual rainfall as shown in Figure 5. For example, at the Lindsay forest site (high rainfall jarrah forest) fine surface fuels reach about  $8 \text{ t ha}^{-1}$  some 6 years after fire, whereas it takes about 10 years at the Yendicup forest site (low rainfall jarrah forest). This is 2–2.5 times the juvenile period of the slowest maturing understorey plants and 3–3.5 times the juvenile period of 90% of plants in these ecosystems. While there is a paucity of information on seed bank dynamics and seed longevity in fire-prone ecosystems, some species are able to produce considerable quantities of viable seed in the first or second flowering years. These include species with short life cycles, such as annual grasses and herbs, species that rely on the production of non-dormant seed to take advantage of post-fire establishment conditions, so mainly flower in the first few seasons after fire (Johnson *et al.* 1994, Denham and Auld 2004) and so-called native 'fireweeds', perennial herbs and shrubs (often leguminous) that regenerate profusely after fire, grow and mature rapidly and are usually relatively short-lived (Bell *et al.* 1989). However other plants, notably serotinous and partially serotinous *Banksia* species, produce low levels of viable seed in the first few years after flowering (Kelly and Coates 1995, Enright *et al.* 1996, Wooller *et al.* 2002). Gill

and Nichols (1989) and Burrows and Wardell-Johnson (2003) have recommended that, for plant conservation, the conservative minimum interval between lethal fires for a particular ecosystem should be twice the juvenile period of the slowest maturing fire-sensitive plant species in the ecosystem, where juvenile period is the time taken for at least 50% of the population to reach flowering age. This 'rule of thumb' is consistent with the limited number of seed bank dynamics studies that have been conducted in fire-prone environments including south-west Western Australia (see review by Burrows and Wardell-Johnson 2003). Therefore, in forested uplands and other flammable habitats within the landscape, the conservative minimum fire interval between lethal fires is about 6–8 years, depending on the productivity of the site (Fig. 2). However, in less flammable parts of the landscape (rock outcrops, riparian systems, some wetlands), where plants with longer juvenile periods are most likely to occur, the conservative minimum interval between lethal fires is probably 10–12 years.

Fire-sensitive plants with long juvenile periods can survive shorter fire intervals if fires are of a very low intensity (non-lethal to the plant) and patchy (do not burn the plant population). Such fires are only possible when burning conditions are near the threshold for fire spread, that is, when fuel quantities are low (Fig. 5), or when fuels are moist. Low fuel quantities can only be maintained by the frequent introduction of fire into the landscape. Frequent patch-burning of the landscape should eventually result in a fine scale mosaic of patches of vegetation at different post-fire stages, ranging from recently burnt to long unburnt. This proposition requires further investigation in the field. South-west landscapes are a mosaic of a variety of landforms and associated vegetation assemblages, including habitats that contain plants with long juvenile periods requiring longer intervals between fires. As these habitats are less flammable, either because they remain wetter for longer, or contain less flammable fuel complexes, prescribed

burning can be planned and implemented under seasonal and diurnal weather conditions to exploit these temporal and spatial flammability differentials, thereby reducing the risk of burning fire sensitive species and communities too frequently. In south-west forest landscapes, low intensity prescribed fires set under moist conditions in spring usually burn the drier parts of the landscape, such as forested uplands, but often do not burn riparian zones and areas of sparse fine surface fuels such as rock outcrops. The proportion of the landscape that is sufficiently dry to burn increases rapidly with the onset of summer drying and where fuels are continuous, fires in summer and autumn usually burn the entire landscape.

## Conclusion

Juvenile period can be used as a biological indicator to help determine ecologically acceptable minimum intervals between fires in various ecosystems. The post-fire juvenile period of understorey plants in south-west forests and associated ecosystems reflects site productivity, as expressed by rainfall, and habitat flammability, as determined by seasonal moisture regime and fuel characteristics. Plants with longer juvenile periods are most likely to occur in the lower rainfall regions, and in less flammable habitats such as riparian zones, rock outcrops and some wetlands. At the landscape scale, the minimum ecologically acceptable fire interval will vary across the landscape in response to changing habitat types. In the interests of plant conservation, fire management, particularly the interval between prescribed fires, should aim to accommodate this variability.

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# Ichnological studies of the Western Australian soldier crab *Mictyris occidentalis* Unno 2008: correlations of field and aquarium observations

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## Abstract

The Western Australian soldier crab, *Mictyris occidentalis* Unno, spends most of its life cycle infaunal in sandy tidal environments, and produces up to 16 different types of ichnological products: back-filled burrows, cavities, circular pustular structures, clots, craters, dactyl prints, discard pellets, eruption structures, excavation pellets, exit holes, hollow shafts, linear pustular structures, mat pustular structures, rosettes, scrape marks, and surface-parallel tunnels (with their floors and roofs). These are the result of the crabs working the sediment at different stages of their life cycle, whether or not they emerge, and their working of the sediment at different times of the tide. Soldier crabs have three phases to their ichnological behaviour corresponding to their life stages. Newly arrived recruits and juvenile crabs are cryptic, and develop sediment surfaces strewn with clots. Crabs in the early to middle stage of their life cycle also are cryptic, and develop subsurface cavities during high water, and subsurface cavities and sediment surfaces covered in pustular structures during low water. Adult crabs exhibit cryptic and emergent phases, and develop the most complex range of ichnological products – during high water, they form subsurface cavities, and during low water they develop cavities in the subsurface as well as sediment surfaces covered in pustular structures, exit holes, dactyl prints (sometimes), discard pellets, and rosettes. Mapping of crab activity and the boundaries of their workings at various scales shows there was a variability in crab behaviour as to whether adult crabs emerged or not, whether working of the sediment surface took place, where in the population emergences or subsurface workings took place, and in the subsurface whether the crabs were active or inactive. Similar variability in crab behaviour was observed in the aquarium. Our study showed a direct correlation between field and aquarium ichnological patterns, and the aquarium observations provided explanation of the field results.

**Keywords:** soldier crab, *Mictyris occidentalis* Unno, aquarium, ichnology

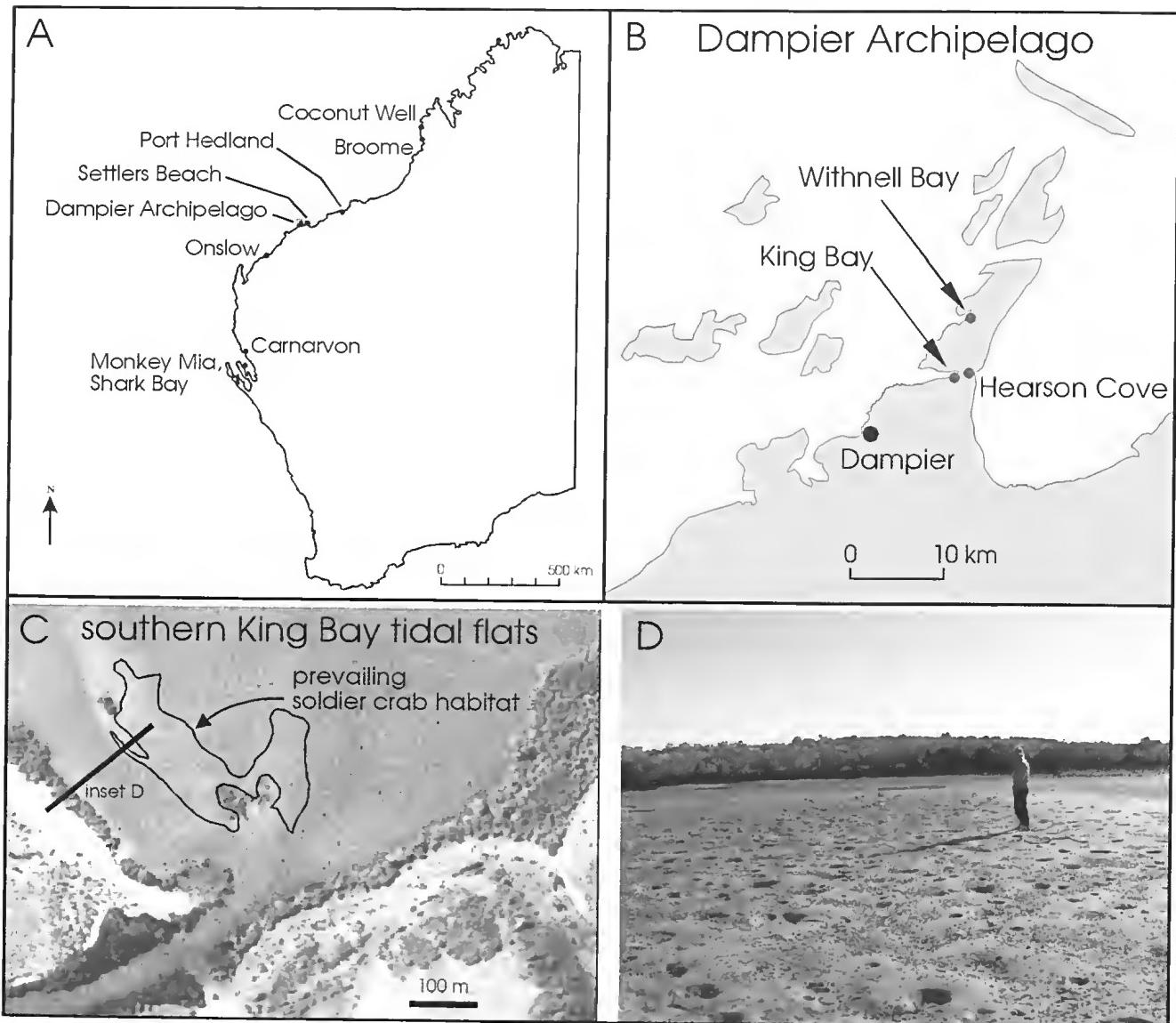
## Introduction

The soldier crab *Mictyris occidentalis* Unno occurs extensively along the coast of Western Australia between Shark Bay and the Broome region (Fig. 1). The prevailing perception is that this crab, in common with other soldier crabs belonging to *Mictyris* elsewhere in the world, forms “armies” emergent above the sediment surface (Cowels 1915, Cameron 1966, Yamguchi 1976) and, indeed, while there is a part of the life cycle of *M. occidentalis* where it does present itself for part of the low tide as vast numbers of individuals at the surface, in fact the species spends most of its life infaunal (cryptic) in the substrate. However, whether infaunal, or emergent for short periods, this crab leaves a plethora of biogenic sedimentary structures as evidence of its complex behaviour that is useful information in the construction of its life stages and various activities it undertakes, and in interpreting fossil evidence of the species.

Ichnology is the study of animal traces, particularly those of fossil organisms (Frey 1975; Ekdale *et al.* 1984; Bates & Jackson 1987). Students of modern sedimentary

environments began to apply the term “ichnology”, originally defined for fossil traces, to modern traces, and as a result, the distinction between modern and fossil traces became blurred. More recently, the discipline of ichnology has been formally subdivided into neoichnology (the study of modern traces [Garrison *et al.* 2007]), and palaeoichnology (the study of fossil traces). We use the term “ichnology” in the sense that it is the study of traces, and that it is an umbrella term to encompass both “neoichnology” and “palaeoichnology”. However, throughout the paper, while the terms “ichnology” and “ichnological” are used, the reader should be aware that products of the modern soldier crab fall into the realm of neoichnology.

Ichnology has long been an important discipline in the tool kit of zoology. The identification and description of species-specific mammal and reptile burrows, seats and other traces, for instance, have assisted in the surrogate identification of the presence of species, and to interpret their behaviour (Triggs 2004; Southgate 2005; Thompson & Thompson 2007a, 2007b). Similarly, burrows and other traces of invertebrate fauna have been studied as part of their ecology, autoecology, sedimentology and biogeochemistry, especially in tidal marine environments



**Figure 1.** Location of study sites. A. General location of soldier crab *M. occidentalis* along the Western Australian coast (grey line), and location of study sites. Note that the occurrence of *M. occidentalis* will not be continuous along the coast but related to available habitat. B. Location of study sites in the Dampier Archipelago region. C. Location of soldier crab habitat in southern King Bay, the Dampier Archipelago. D. Surface of habitat in southern King Bay showing stingray-pocked surface.

(Frey 1975; Reineck & Singh 1980; Carney 1981; Ekdale et al. 1984). All such ichnological studies, whether of vertebrate or invertebrate fauna, have provided invaluable insights into the ecology, autoecology, and animal-habitat relationships for those species investigated (McCall & Tevesz 1982), and the more detail that has been garnered, the more insights have flowed from such work.

To our knowledge, to date, no studies have comprehensively described the ichnology of *Mictyris*, i.e., all of its burrowing, foraging, and trace-producing activities. If they have any ichnological component in their scope, most studies have focused on only one aspect of soldier crab ichnology (such as its burrow structure; Cowles 1915; Takeda & Murai 2004), or have briefly described ichnological products as background information to autoecological studies (Quinn 1983; Rossi & Chapman 2003) and ecological impact studies

(Dittmann 1996; Sadao 2001; Sadao 2002; Webb & Eyre 2004). We suggest that ichnological features in their own right are important aspects of the soldier crab life history and autoecology. A study of soldier crab ichnological features can assist researchers in a number of ways, e.g., to determine the presence of soldier crabs even though they may not be emerging during a particular (settlement or early to middle) stage of their life cycle, to determine what is the predominant life stage of the population at the time of observation (qualitatively determining the relative abundance of juveniles to adults), and to determine the extent of patchy crab foraging activity on the tidal flat, and hence information about crab behaviour. Ichnology and ichnological products also form the basic temporal and sedimentologic framework to designing further studies on soldier crabs in regards to crab-and-sediment relationships, soldier crab predator associations, relationships and responses, soldier crab

accessing and processing of food, nutrient recycling, and geochemistry, amongst others.

In this project, the need for laboratory/aquarium studies grew from field observations and experiments where it became difficult to determine and explain the apparent lateral movement of soldier crab populations suggested by the patchy patterns of activity of the populations, and the various patterns of the biogenic traces. The aquarium studies added to and corroborated field observations, allowing proper interpretation of the latter since the crabs in the aquarium directly and unequivocally replicated ichnological patterns observed in the field. Also, the aquarium studies provided insights into soldier crab behaviour not readily apparent on the tidal flat, such as behaviour during times of inundation at high tide. The results of the field and ichnological aquarium studies additionally provided data to interpret the former presence of the soldier crabs from their traces. Such information is useful in interpreting Pleistocene tidal flat rocks, and (earlier) Holocene beach rocks, thus pointing to the presence of *Mictyris* populations in the past.

Previous work on crab behaviour in aquaria has been undertaken for other species, e.g., those of *Dotilla*, *Uca*, and *Portunus* (Palmer 1973; Avent 1975; Crane 1975; Phillips & Cannon 1978; Furota 1996; Takeda *et al.* 1996; Nakasone & Murai 1998; Pope 2000; Rodriguez *et al.* 2000; Yamaguchi 2001; Arshad *et al.* 2006; Koukkari & Sothern 2006), and they have been useful in documenting biorhythms of particular species with respect to tidal cycles and useful to studies of other behavioural aspects. Some studies have been undertaken on species of *Mictyris* in the aquarium, but these have tended to focus on physiological aspects of a given species (Kelemeec 1979; Quinn 1986; Maitland & Maitland 1992; Ahsanullah & Ying 1993; Henry 1994), or in the laboratory/aquarium to document some particular burrowing behaviour (Cowles 1915; Takeda & Murai 2004). To date, no studies have involved the ichnology of *Mictyris* in the detail of the aquarium study presented here.

We also draw attention to the work of Knox & Miller (1985) who similarly used aquarium studies to correlate with and interpret field observations, and showed that the one organism can produce a range of ichnological products (though the variability of the ichnological products in their study was not due to variable behaviour, as is the case in our study, but to the organism interacting with a variable sediment). Using gastropods, Knox & Miller (1985) investigated the environmental controls on the gastropods' trails and showed that different morphology could be generated under different environmental conditions. In the aquaria, with sediment of various grainsizes, composition, and consolidation, they found that the one species of gastropod produced trails that varied in depth (of ploughing), cross-sectional shape, and traverse ridging. The authors could relate these laboratory results to tidal flat sub-environments that also varied in sediment properties.

The purpose of this paper is to comparatively describe behaviour and the variety of the ichnological products of *Mictyris occidentalis* in the aquarium and on the tidal flat, and to describe those traces useful to interpreting *M. occidentalis* behaviour and life patterns in the field. The paper begins with description of the behaviour of

the crabs on the tidal flat to provide a background setting for the species, and the types of ichnological products that the crab generates, as a baseline for what to expect and what to explain in the aquarium studies.

In this paper, we describe the ichnological patterns of the Western Australian soldier crab in the field and in the aquarium to a level of detail not previously provided for a Western Australian tidal-flat marine organism. This was undertaken because *M. occidentalis* yields a complexity of ichnological products that, in addition to being genus-specific, reflects its ontological stage, and complex behaviour related to the stage of the tide. The results have been invaluable, supplementing studies in the biogeography, ecology, and autoecology of *M. occidentalis* in Western Australia.

## Terms and definitions

Since soldier crabs, as a result of their unique behaviour in their subsurface feeding and surface foraging, leave characteristic imprints on the tidal flat as various structures which can later become palaeoichnological traces, it is necessary to define appropriate terms. Some soldier crab-created structures can be related to terms already existing in the general literature, e.g., back-filled burrow, while terms employed for *Mictyris* biogenic structures by other authors are briefly mentioned and if they are not employed here, reasons are given. The terms used in this paper are presented with definitions in Table 1.

## Materials and methods

Methods involved a field work component and a laboratory component. Field work was focused on a sandy tidal flat in southern King Bay, Dampier Archipelago, Western Australia (Fig. 1). In order to replicate the natural environment of the soldier crab as near as possible in the aquarium, field work involved description of the natural setting of the soldier crab habitat in terms of sediment type, documentation of the micro-topography, depth to the water table at the habitat, frequency of tidal flooding (inundation), temperature of the water, and density of population. Field work was supplemented by observations and photography of soldier crab ichnological products in the following additional sites in Western Australia: Shark Bay, Onslow, Maitland River Delta, Withnell Bay and Hearson Cove (in the Dampier Archipelago area), Settlers Beach (Cape Lambert area), Port Hedland, Broome, and Coconut Well (north of Broome).

In the field, the subsurface and near-surface crab traces were documented by excavations and planing of the surface. Crab activity in pelletising the surface, or creating a pustular surface was documented by video camera and still photography. Observations were undertaken mostly during the day-time low tide, and 10 night-time low tides. To determine the depth at which the crabs resided in the subsurface, we undertook excavations, as well as coring with 10 cm diameter PVC pipes to 1 m depth (to extract *in situ* sediment with crabs therein), box coring to 30 cm depth, and systematic planing of the surface.

**Table 1**

Terms and definitions employed in this paper for soldier crab biogenic structures on or in the substrate

Term	Definition in this paper	Previously used terms
back-filled burrow	vertical to horizontal, cylindrical tube generally 10–15 mm diameter, of disturbed sediment; a burrow that has been back-filled with sediment by an infaunal vagile crab	term already established in the ichnological literature
cavity	small, unattached, equant (up to 2 cm across), to linear (up to 4 cm long), air-filled hole in sediment occupied by soldier crab in the subsurface; air bubble may have a thin layer of geopetal muddy water on the bottom during high tide inundation; size of cavity depends upon size of crab; a specialised type of burrow formed in the subsurface by soldier crabs in all stages of their life cycle	burrow; however, the term "burrow" on its own is too broad to be applied to the range of specialised structures described herein; also the term "burrow" often carries implication that the structures are linearly extended; the term "igloo" has been used for a pellet-roofed air-filled chamber just beneath the sand surface for a species of <i>Dotilla</i> (Takeda <i>et al.</i> 1996); this term does not convey the notion of the deeper subsurface cavities encountered in this study, and so is not used here
circular pustular structure	elevated (2–10 mm relief), circular area, 1–5 cm in diameter, composed of packed excavation pellets or packed discard pellets (see below for general "pustular structure"); generated by a subsurface crab not laterally mobile, i.e., formed from below in a single place; isolated, individual pustular structure also referred to as "pustule" in this paper	coined in this paper
clot	small (<3 mm) lump(s) of sand on tidal-flat surface pushed up mainly by a very small juvenile crab (<3 mm) that is residing in a cavity, or feeding just below the sediment surface; clot size related to crab size	coined in this paper
crater	roughly circular raised ring of sand surrounding a central depression, produced by the circular burrowing motion of a crab	coined in this paper
dactyl print	short, narrow impression in fine sand or mud film on sediment surface made by dactyl of walking leg; several dactyl prints in line comprise a track	coined in this paper
discard pellet	single round ball of sand formed from sand filtered in the buccal cavity; it is placed on the tidal flat surface during the surface feeding activity of the crab, or placed from below from within a surface-parallel tunnel onto/into the surface by the feeding activity and/or excavation from the tunnel; size of the pellet depends on crab size – they range in size from 2–5 mm, but tend to be similar in size for a given age group; a crab with a carapace length of 6 mm will construct a pellet of 2 mm, and a crab of carapace length of 15 mm will construct a pellet of 5 mm	pseudofaecal pellet (Cameron 1966, Quinn 1983); this term is not used in this paper as it describes not what the ichnological product is, but what it resembles
eruption structure	flange or lip of sand surrounding an exit hole	coined in this paper
excavation pellet	single round ball of sand formed by the crab as it excavates sediment usually to form a surface-parallel tunnel; the ball of sand is placed from below onto/into the surface, with other such pellets, to form the roof of the subsurface tunnel; size of the pellet depends on crab size – they range in size from 2–8 mm; generally, the excavation pellet is not as cohesive as a discard pellet	coined in this paper
exit hole	circular opening 5–15 mm in diameter created by a crab exiting the substrate and commencing surface activities; may be on the undisturbed sediment surface or within a pustular structure	coined in this paper
hollow shaft	vertical or inclined tunnel to the surface 20–50 mm long and up to 10 mm diameter generally constructed by adult crabs; may be manifest at the surface by an exit hole or a rosette, or a pustular structure; a specialised type of burrow formed by a crab exiting the sediment	burrow; however, the term "burrow" on its own is too broad to be applied to this specialised soldier crab structure
linear pustular structure	elevated (2–10 mm relief), linear, oblate, to sinuate, to multifurcate area composed of packed discard pellets and excavation pellets (see below for general "pustular structure"); they are 1–3 cm wide and up to 20 cm long; generated by a subsurface crab that is laterally mobile; isolated, individual linear pustular structure also referred to as "linear pustule" in this paper	coined in this paper

Table 1 (cont.)

Term	Definition in this paper	Previously used terms
pustular structure	general term for any elevated (2–10 mm relief), circular, linear, oblate, to sinuate, to multifurcate, or matted area composed of packed discard pellets and excavation pellets; three types are recognised: (1) circular types; (2) linear, oblate, to sinuate, to multifurcate types; and (3) mat types; isolated, individual pustular structure also referred to as “pustule” in this paper	hummock (Quinn 1983; Webb & Eyre 2004); we use the term hummock to describe the macroscale mounds on the tidal-flat surface produced by stingray feeding
mat pustular structure	elevated (2–10 mm relief) area of disturbed sediment composed of coalesced circular, linear, oblate, to sinuate, to multifurcate pustular structures; the mats can range in size from <i>circa</i> 20 cm to tens of metres	coined in this paper
rosette	isolated, somewhat circular, raised mound, usually 3–4 cm in diameter, comprising a central plug and an outer ring that has a vague radial structure; formed by crab burrowing into the sediment for re-entry, excavating and disposing of the sand radially as it corkscrews into the sediment	mound (various authors)
scrape mark	short linear scratch in sediment surface where a crab has scraped up sand with its cheliped to pack into the buccal cavity	generally used term for other tidal flat crabs
tunnel	shallow linear, sinuate, to multifurcate surface-parallel structure, 1–4 cm wide; composed of a floor excavated from the underlying sediment, and upper part enclosed by a pustular roof; formed by crab working in the near-surface forming a surface-parallel trough enclosed by a pustular roof	gallery (Webb & Eyre 2004): has connotations of a passage with at least one open side; it is not considered to be appropriate to describe this totally enclosed soldier crab structure
tunnel floor	the basal concavity of a tunnel, excavated from the underlying sediment	coined in this paper
workings	any soldier crab biogenic structures on the sediment surface; so termed because the sediment has been “worked over” by the soldier crab	coined in this paper

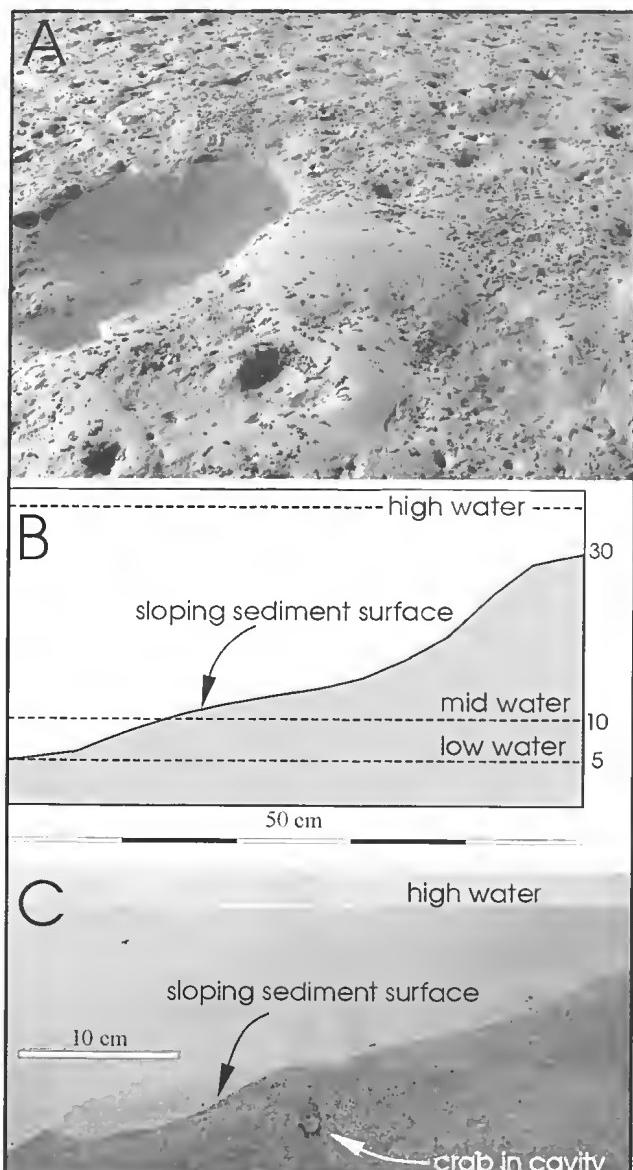
For the aquarium observations, a glass aquarium (50 cm × 30 cm by 30 cm deep) with a basal outlet valve was set up, and sediment from the soldier crab habitat at King Bay tidal flat was placed therein to create a sloping surface, with 30 cm depth of sediment at one end of the aquarium and 5 cm at the other end, mimicking the sloping edge of a stingray feeding excavation hollow (Fig. 2). Thirty soldier crabs from the King Bay site were placed in the aquarium, replicating the density of the crabs in the natural environment. The crabs and sand were covered in seawater. The seawater was changed every two days. Sediment in the aquarium was left to oxygenate and deoxygenate with the processes of water exchange, crab burrowing, and crab inactivity, so that effectively the subsurface sand replicated the natural environment of the tidal flat, in contrast to Kelemeć (1979) who oxygenated the sand in an aquarium experiment by diffusing oxygen from below.

Four aquarium experiments were conducted. The first was in the field for one week for the purpose of determining whether soldier crabs could survive aquarium conditions and to determine on a preliminary basis their response to aquarium conditions. In the field, the aquarium and its sediment content rested on a sand mound on the tidal flat surface so that it was naturally inundated twice daily by spring tides (at low tide, the water in the aquarium was siphoned off to simulate low tide). The second aquarium experiment was carried out in a laboratory in Perth for 9 months with the aim of observing soldier crab behaviour and documenting biogenic structures by observation, mapping of aquarium walls, and intensive video camera filming and still photography. The third aquarium experiment was

carried out in a laboratory for 3 months with the aim of further intensive photography. The last experiment was carried out in a laboratory for 1 month with the purpose of observing bioturbation in layered sediment.

In the first experiment, in the field, the temperature of the water, sediment and air was the same as ambient environmental conditions. In the second experiment, the temperature of the seawater was regulated by a heater, bringing the water temperature to *circa* 25°C. In the third, the entire aquarium system was placed in a temperature-regulated room in which air temperature and water temperature were kept to 28°C. In the fourth, the experiment was conducted during the Perth summer, and the temperature was not regulated. In this way the laboratory aquarium experiments, which ran for a total of 13 months, were conducted over the Perth summer and winter, without winter temperatures affecting the crabs.

Over the time of the experiments, twice daily, and daily for several days every fortnight, seawater was placed in the aquarium for half a day, and then emptied to replicate semi-diurnal spring tides and neap tides. One low tide was simulated during the day-time, and one during the night-time. Every month, to replicate maximum neap tidal conditions (that were documented at the soldier crab habitat in King Bay), the aquarium was left inundated for two days. The water in the aquarium was emptied and replenished either by siphoning, or by basal efflux from the tank through the outlet valve (Fig. 1). With the siphoning or the efflux of water from the aquarium to simulate a low tide, two levels of water were achieved (Fig. 2): 1. the water level was brought down to 5 cm from the base of the



**Figure 2.** Experimental design. A. Basis for the geometry of the sand in the aquarium – field photograph of a stingray-generated water-filled hollow, with its adjoining mound of sand. B. The three levels of water attained in the aquarium; at high water, all surfaces are flooded; at mid water, simulating a neap tide, the water table is 20 cm below the high point of the sand; at low water, simulating a spring tide, the water table is 20–30 cm below the high point of the sand. C. Portion of the side view of the aquarium at high water, with the sloping sand surface simulating the hollow-to-mound relationship shown in A.

aquarium, with the water table 25 cm from the surface of the sand at the upper slope to simulate maximum spring tide conditions; and 2. the water level was brought down to 10 cm from the base of the aquarium, with the water table 20 cm from the surface of the sand at the upper slope to simulate moderate spring tide conditions. For the latter situation, a pool of water was left at the lower slope of the sand.

Once it became apparent from aquarium observations that the crabs, as a result of their subsurface activities, were producing structures *within* the sediment as well as on the sediment, in the fourth set of aquarium

experiments the sand was artificially laminated in order to be able to trace the development of biogenic (bioturbation) structures.

The behaviour of the crabs and the ichnological products of the crabs in the aquarium were documented by video camera, by photography of the walls and surface of the aquarium, and by observation and drawings (directly tracing from aquarium walls onto transparent sheets). Most of the observations were undertaken during day-time low water, but several of the night-time low water periods were also documented. For video camera filming, the camera was set up on a stand and allowed to run continuously for 3 hours. For example, for low water activity, as soon as the water was at its low level, the camera was activated and allowed to run for 3 hours continuously. In this manner, there was a record of the onset of the crab activity and its progression. Filming was undertaken of the surface and of one of the aquarium walls. For high water activity, the camera also was run for 3 hours so that there was a continuous record of crab activity as exposed along the aquarium walls. In total approximately 25 hours of film footage was obtained for later analyses.

Additionally, 50 hours also were logged in directly observing the crabs constructing cavities, maintaining cavities, moving vertically upwards to exit (and creating vertical hollow shafts), spiralling downwards to re-enter the sediment, and creating vertical hollow shafts to progress from the surface to lower depths. This was an important component of the study as there was direct observation of the action and the product undertaken and generated by the crabs, respectively.

This study, in terms of observing and experimenting with the soldier crabs in the field, is based on decades of field work. Commencing in 1980, one of us (VS) visited the King Bay site on a quarterly basis between 1980–1982 and 1985–1988 for 2 consecutive days, and on a monthly basis between 1982 and 1985 for 1 day each month, amounting to *circa* 200 hours of observations and experimentation. Commencing in 1997, both of us visited the King Bay site on a yearly to quarterly basis between 1997 and 2007 for 3–4 days at a time, amounting to 40 man-days (or *circa* 200 hours) of observations and experimentation.

Mapping of crab activity and the boundaries of their workings was undertaken using enlarged high-resolution aerial photographs at a scale of 1:500. At this scale, trees, megaripples, creek lines, other tidal drainage lines, and other tidal landforms and features were evident, and were used as medium-scale landscape markers to provide location and orientation for mapping the outlines of crab workings. Between these medium-scale landmarks, boundaries of the workings were established by direct mapping onto the aerial photographs, supplemented by (metre-length) pacing to the nearest metre.

Mapping at the smallest scale of the increase in workings in quadrats was undertaken by photography. A series of fifteen replicate 25 cm × 25 cm quadrats were randomly spread over the tidal flat surface immediately after the tidal flat surface was exposed, and photographed from time zero on a 15-minute basis for a total of 3 hours. These photographs provided the basis

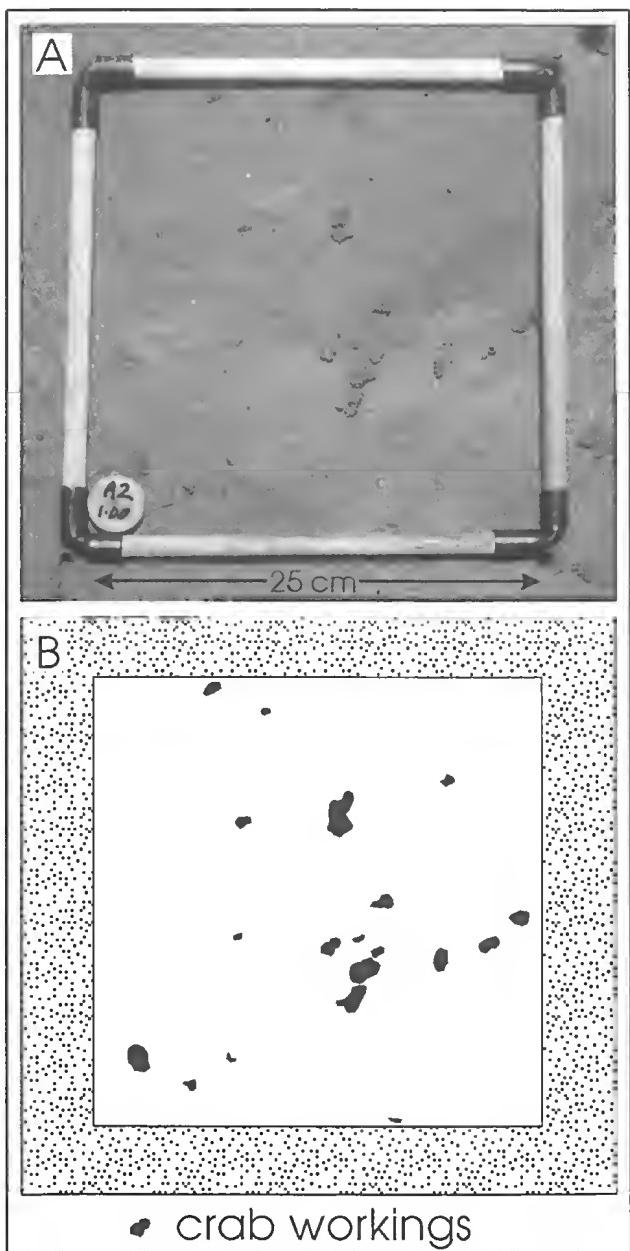


Figure 3. Quadrat (25 cm x 25 cm in size) in the field, with crab workings appearing within the quadrat, and tracing of the workings for use in Figure 5.

for tracing the initiation and progression of the various crab workings such as clots, pustular structures, and rosettes, that appeared on the surface (Fig. 3).

#### The soldier crab habitat in King Bay, Dampier Archipelago

The soldier crab habitat in southern King Bay is a sandy, mid-tidal to high-tidal flat, specifically a sandy ebb-tidal delta located at the mouth of a tidal creek (Semeniuk *et al.* 1982; Semeniuk & Wurm 1987; and Fig. 1). Occurring between levels of *circa* mean low water neap tide (MLWN) and mean sea level (MSL), it is exposed during all spring tides for several hours, and exposed during most neap tides for a few hours, however, on some neap tides the habitat is not exposed

at all. While the habitat receives some low-amplitude waves from the open head of King Bay (Semeniuk & Wurm 1987), the environment is a relatively low-energy site located within the King Bay embayment. In this environment, some mud does accumulate and as such the substrate habitat of the soldier crab is a slightly muddy, fine to medium sand (mean sand grainsize is 125  $\mu\text{m}$  and mud content is *circa* 3%). The sediment has *circa* 0.5% organic matter as detritus.

The surface of the habitat is pocked with 20–50 cm diameter feeding excavations of stingrays, hence in detail the habitat is undulating, composed of a series of pools and low sand mounds (Fig. 1). In general, the water table under the tidal flat on a low spring tide is 10–20 (-30) cm below the surface. Soldier crabs inhabit the undulating sand surface, and more specifically the sand mounds adjoining the pools. Excavations and box cores indicate that the soldier crabs are located in the upper 10–20 cm of sediment surface during low tide periods.

The sediment that underlies the tidal flat where the soldier crab resides is invariably pigmented at shallow depths by iron sulphide. At depths of 10–30 cm and greater, the sediment is medium grey to dark grey. At 0–10 cm, the sediment is medium grey to light grey. The surface layer, <1 mm thick, is commonly oxidised to light grey or a buff/tan tone. Pellets created by the crabs from the shallow subsurface and surface tend to mirror the pigmented sediment from which they are derived.

Crab workings are commonly reworked by tidal currents and small amplitude waves during spring tides. During neap tides, tidal currents are of smaller magnitude, and crab workings have a higher chance of preservation. We have observed soldier crab workings surviving the previous high-tidal current reworking: the workings are not always distinct, but reduced to a series of rounded lumps. Also, following a high tide, especially during neap tide periods, and depending on the sedimentary budget of suspended mud in the region, there may be a thin film of mud or very fine sand on the sediment surface, the thin film of mud being deposited as a result of lag / settling lag processes (*cf.* Postma 1967; Reineck & Singh 1980); during these times, soldier crab ichnological products stand out in contrast, and dactyl prints and tracks are best preserved.

#### Field observations

Soldier crabs in the field exhibit a range of trace activities, as determined by direct observation and excavations. Figures 4–6 illustrate a range of structures produced by the soldier crabs from tidal flat settings.

At King Bay, but supplemented by observations elsewhere, soldier crabs spend most of their life cycle as in-fauna in the sandy environment. There are three phases to their ichnological behaviour corresponding to their life stages:

1. newly arrived recruits and juvenile crabs in the early stage of their life cycle – a cryptic phase;
2. crabs in the early to middle stage of their life cycle – a cryptic phase; and
3. crabs in the adult stage – exhibiting cryptic and emergent phases.

Immediately after the ebb tide exposes the surface, the sediment is still very wet and there is an absence of scrape marks and soldier crab dactyl prints, even though there is the opportunity for preservation of such traces because of the thin film of mud on the sediment surface formed by scour lag / settling lag processes. Such mud can preserve surface traces and activities of fauna, e.g., the activities of fish feeding. This indicates that there was no soldier crab surface activity during the high tide.

Crab ichnological activities are described below, focusing on those that occur at low tide. During a low tide, in all cases the crabs begin their activities that are manifest as ichnological products on the surface when the sand is exposed long enough (within one to two hours) for it to drain free of phreatic interstitial water, but is still cohesive with pellicular moisture. This occurs during day-time low tides and night-time low tides.

When a population is composed of newly-arrived recruits (sizes 1–2 mm) and/or individuals in the early (juvenile) stage of their life cycle (sizes 2–3 mm) [composed of very small, almost translucent crabs, and grey-blue juvenile crabs], during a low tide the surface becomes speckled with small clots of sand as a result of settlement and juvenile recruit workings (Fig. 4A). Generally, these crabs remain in the subsurface, and in excavating a small hole (cavity) therein, dispose of the sand onto the surface as a small aggregate *circa* 1–2 mm in size. These are scattered on the surface above the individual crabs. At this stage, the crabs may also create craters (Fig. 4B). They do this by opening the roof of their near-surface cavity exposing themselves to the surface, and excavating and depositing excavation pellets as a ring of sand around the opening; later, when the crabs descend to lower depths, they will fill the central concavity from below with more excavation pellets, leaving a single circular pustule where the crater once was.

When a population is in the early to middle stage of their life cycle (sizes 3–5 mm), composed of grey-blue juvenile and sub-adult crabs, during a low tide the surface becomes "pustular" as a result of crab workings. Again, the crabs remain in the subsurface, but their workings are the result of their creating shallow, meandering surface-parallel tunnels, the roofs of which are a mass of small cohesive pellets of sand, formed as a consequence of their feeding and excavation activity. In the first instance, cryptically, within 1–2 centimetres of the surface, the crab scrapes and excavates a proportion of sand from the near-surface, places it in its buccal cavity to extract its food, then rolls the food-depleted sand into a small ball, 2–3 mm in size, which it jettisons as a discard pellet to one side or attaches it to the roof of the developing tunnel. Some of the pellets are also formed by excavation and aggregated into the roof as balls of sand (excavation pellets). For the discrete surface pellets, the term "discard pellet" is used to make a distinction from the feeding pellets of crabs such as *Scopimera*, which aggregate sand on the surface into small balls or pellets from which they extract food particles. As a result of this soldier crab activity, the upper 1–2 centimetres of the sand is transformed into a labyrinth of tunnels the roofs of which are constructed of the material excavated from the tunnels. As such, the sediment surface becomes generally composed of linear to meandering areas of

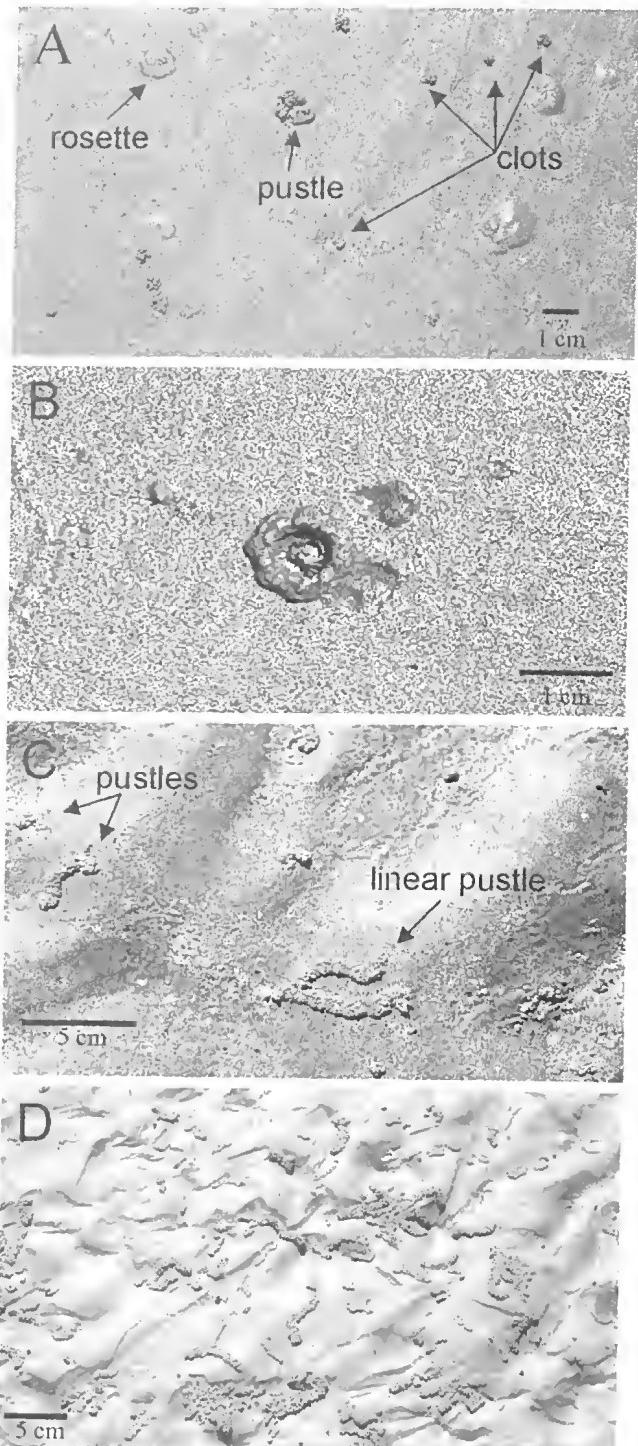
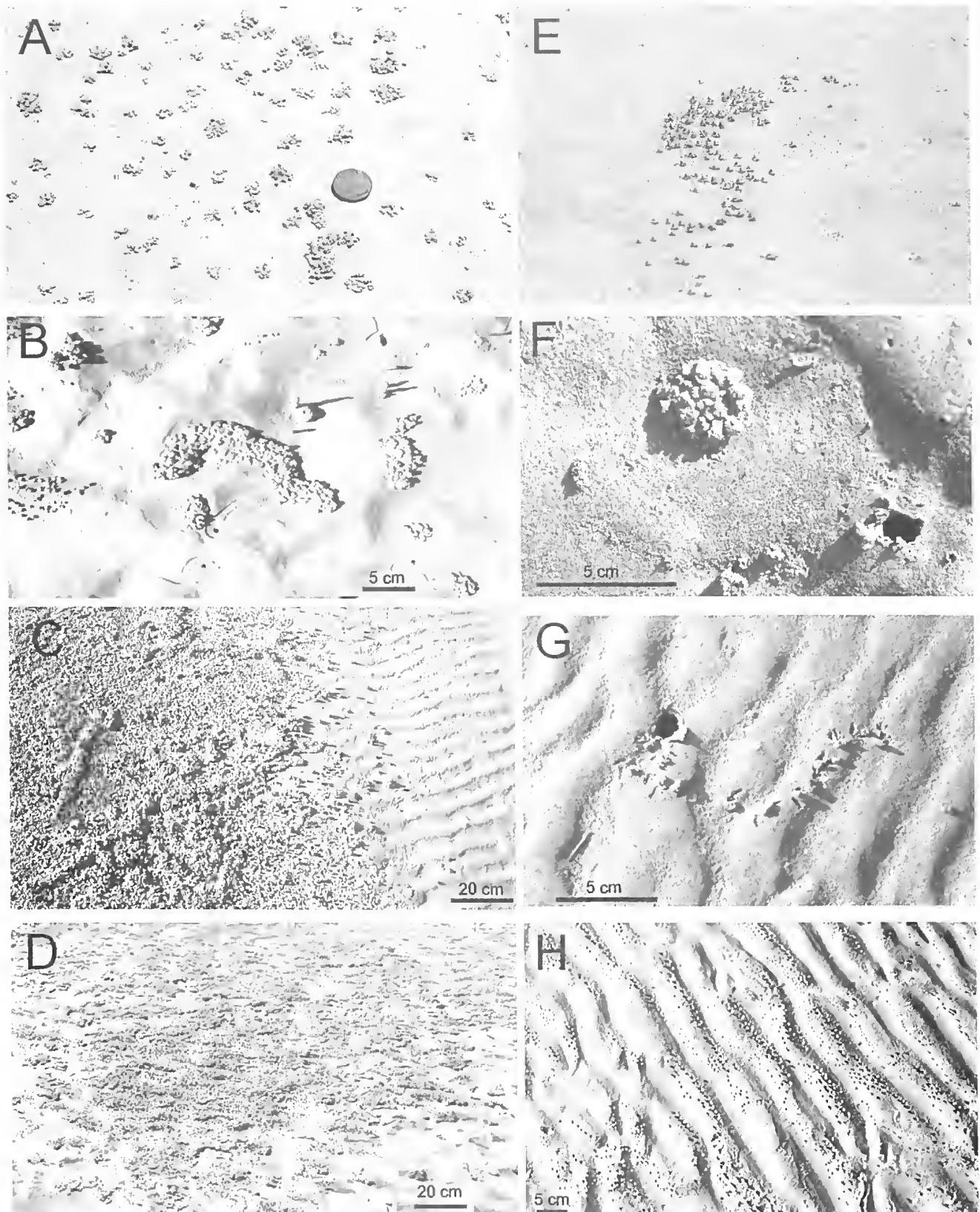
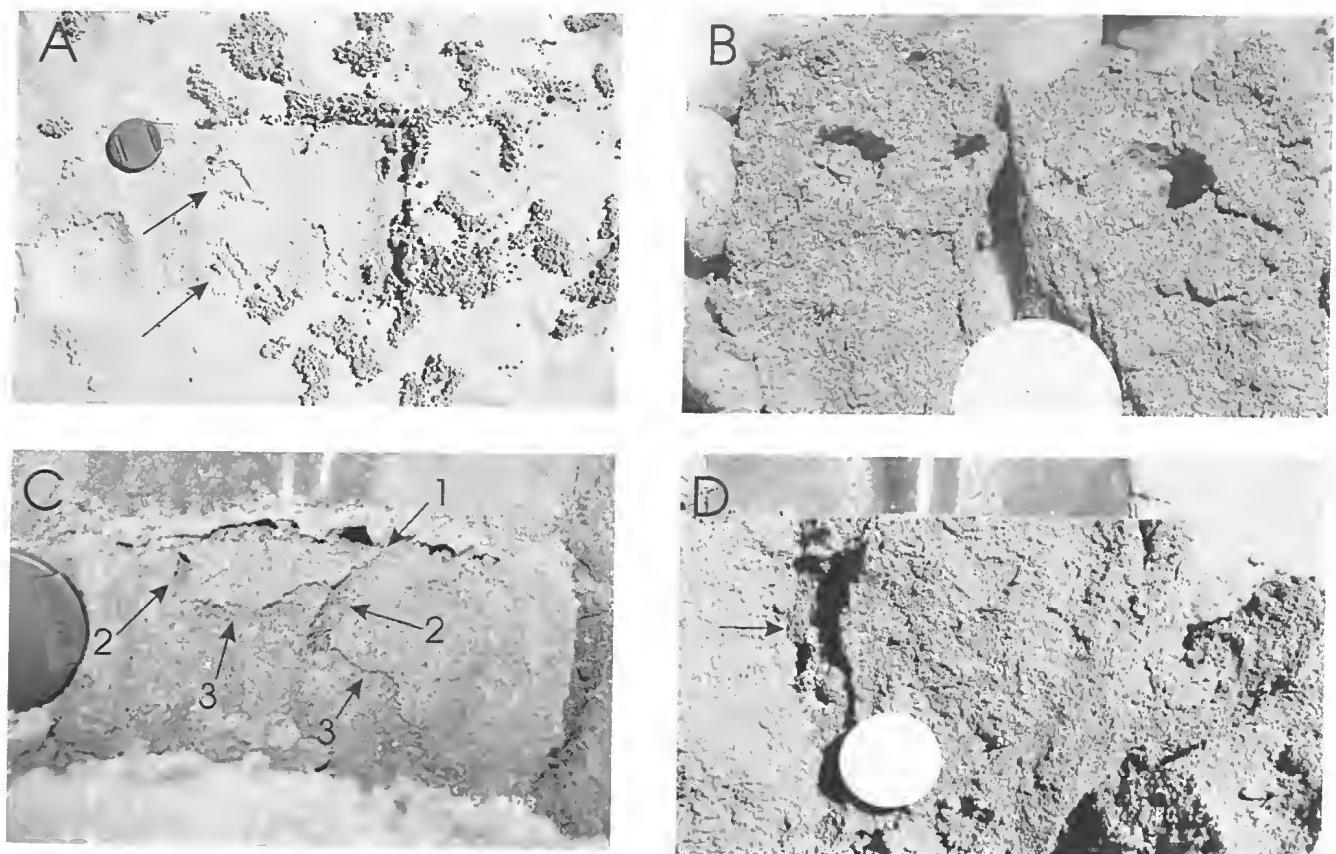


Figure 4. Photographs of types of surface workings by crabs of the settlement phase and juveniles. These workings are generated by crabs mostly working in the subsurface. A. Overview of a field of clots. B. Crater, with crab present in the central concavity. C. Circular pustular structure and linear to meandering pustular structures. D. Overview of a more complex field of linear to meandering pustular structures.

pustular sand, and elevated by 2–10 mm above the former sediment surface as the material of the tunnels is transferred to the roofs (Figures 4C and 4D). Thus the roofs of the tunnels are composed of aggregated discard pellets and excavation pellets of sand. Carefully removing the cover of sand pellets exposes the surface-



**Figure 5.** Photographs of types of surface workings by adult crabs. These workings are generated by crabs working the sediment in the subsurface and on the surface. A. Field of circular pustules (lens cap is 50 mm diameter). B. Circular pustular structure and meandering pustular structures. C. Zone of soldier crab workings adjoining a rippled sand flat; the workings consist of a mat of pustular structures generated by coalescing, circular pustular structures and meandering pustular structures, and discard pellets. The majority of the workings are discard pellets. A prominent meandering pustular structure is evident to the middle left of the photograph. D. A mat of pustular structures generated by coalescing (mainly) meandering pustular structures and circular pustular structures; discard pellets are also common. E. Swarm of soldier crabs walking over a tidal flat sparsely covered in discard pellets. F. Exit hole with eruption structure, and (re-entry) rosette. G. Exit hole with eruption structure, and a trail of scrape marks with discard pellets. H. A row of discard pellets along the crests of ripples, where the soldier crab was preferentially walking.



**Figure 6.** Excavations in the field to illustrate soldier crab ichnological structures. Lens cap in A and C is 50 mm diameter; film cannister cap in B and D is 35 mm diameter. A. Planed surface to remove the pustular structures to 1 cm depth to reveal the underlying horizontal tunnels. Arrows show tunnels below the surface. B. Equant cavity located *circa* 2 cm below the sediment surface. C. The tunnel under a pustular roof (arrow 1), hollow shafts (arrow 2); arrow 3 points to artificially generated cracks. D. A hollow shaft leading up to an exit hole.

parallel labyrinth of tunnels (Fig. 6A). The activity of the crabs in constructing the shallow surface-parallel tunnels mainly begins some 30 minutes to *circa* 60 minutes after the tide has fallen low enough that the water table is 10–20 cm below the sediment surface, and as a result, the water in the sediment changes from phreatic to pellicular water. Once it begins, the activity of producing the tunnels and creating a pustular surface continues for up to 150 minutes depending on the phase of the tidal cycle (Fig. 7). Figure 7 shows the increase in surface workings in time for 5 quadrats. In this instance, while there were workings evident as pustular structures, and even though the crab population was adult, there were no emergences of crabs during this particular low tidal period.

As the crabs work the immediate subsurface for food, the surface aggregations of pustular structures become longer and begin to coalesce. The end result may be a tidal flat surface completely covered in pustular structures that appear like a mat on the surface.

Because the discard pellets and excavation pellets that comprise the tunnel roofs are derived from sediment > 1 mm in depth and are deposited into the surface sediment, there is a contrast in colouration of the meandering to linear pustular structures. These pellets tend to be light grey to mid-grey amidst a surface tone of buff/tan and light grey, hence they stand out in tonal relief. Having a higher moisture content than surface

sand, these pellets from the subsurface have a less well-defined spherical shape.

During this stage of the crab population's life cycle, the crabs also construct cavities which are separate from the surface-parallel tunnels. Excavations expose centimetre-sized, rounded to equant cavities located 1–5 cm below the surface. As mentioned earlier, these cavities are holes in the sand but with a geopetal lining of mud on their floor.

When soldier crabs are in the adult stage of their life cycle (sub-adult and adult, sizes 7–10 mm, and up to 16 mm, with the population composed of deeper blue to sky blue soldier crabs), during a low tide three types of activity ensue: 1. the surface becomes pustular as a result of crab workings composed of circular pustules (Fig. 5A), or linear/meandering pustular structures (Figures 5B and 5C), and the surface, with intensive working over by the crabs develops into a pustular mat (Figures 1D and 5D), as described earlier; 2. some crabs also may construct cavities; and 3. a proportion of the resident adult population emerges.

When the crabs emerge (Fig. 5E), there is an abundance of exit holes which are circular, often with eruption margins (Figures 5F and 5G). Emergent crabs wander on the surface feeding. Thousands may emerge in this manner, feeding and creating the impression of the soldier crab "armies" (Fig. 5E). Crabs have been documented emerging mainly during day-time low tides, but there are

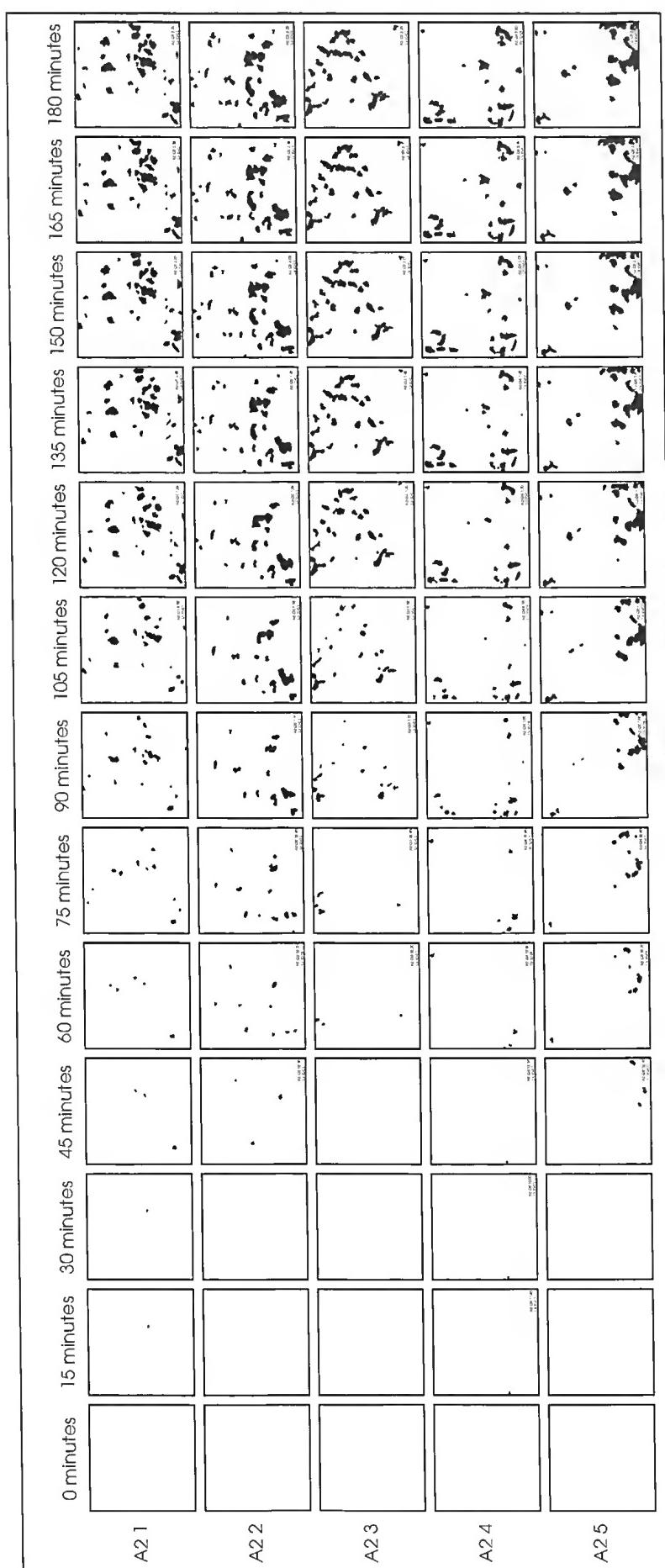


Figure 7. Increase in density of workings in five quadrats over 3 hours. In quadrats A2.1 and A2.4, one circular pustular structure appears at 15 minutes; at 45 minutes, circular pustular structures have appeared in four of the quadrats; by 90 minutes the workings have become conspicuous; most workings have ceased by 120 minutes. Quadrats are 25 cm x 25 cm.

exit holes evident during some of our night-time observations, though no observations of mass swarming. When the crabs emerge and forage on the surface, they generate scrape marks (Fig. 5G) in their harvesting of sediment for extraction of food, and the surface becomes covered in small discard pellets (Figures 5G and 5H). Several scrapings may be undertaken before the crab accumulates enough sediment in its buccal cavity to discards a pellet of sand. The discard pellets are placed a short distance away from where the sand was scraped. Depending on whether the crabs are relatively slowly wandering in their foraging, or rapidly moving over the surface, this distance can range from 5 mm to *circa* 25 mm, and locally up to 100 mm. Depending on how mobile the crab has been during feeding, the discard pellets can be arranged in meandering lines, or randomly, or in localised patches. Sometimes, ripple crests exert a control on the direction of crab wandering, and the line of discard pellets follows the ripple crest. (Fig. 5H).

The discard pellets, derived from the oxidised surface sand that has lower moisture content than the underlying sand, tend to be tan/buff in colour, similar to the surface sediment, and are more cohesive as spherical balls. They contrast with the colour of the pellets that comprise the meandering to linear pustular structures, hence they are conspicuous. Depending on the abundance of emergent crabs, and for how long they stay emergent, the surface may be littered with scattered discard pellets, or densely packed with an abundance of such pellets.

Dactyl prints are locally present when there is a thin film of mud or very fine sand on the sediment surface, but this ichnological feature is not common.

Eventually, the crabs re-enter the subsurface and do so by corkscrewing into the sediment, producing a distinct rosette pattern (Fig. 5F). As the crabs corkscrew in, they excavate the sand and pile it to one side as they rotate inwards, thus producing a rosette of excavated material (hence the vague radiating structure to the rosette), and finally as they descend to a level below that of the surface sediment, they upwards pack the central hole so that the final morphology of the trace commonly is a rosette of excavation discards and a central plug (Fig. 5F). Crabs were observed corkscrewing in both clockwise and anticlockwise directions, showing no sign of "handedness".

When the crabs rapidly exit or re-enter the sediment, they may leave vertical to near-vertical holes.

Figures 6B–6D illustrate a range of subsurface structures developed by the crabs. Figure 6B illustrates an equant cavity located *circa* 2 cm below the sediment surface. Figure 6C illustrates hollow shafts, and the tunnel under a pustular roof. Figure 6D illustrates a hollow shaft leading up to an exit hole.

At the stage where adult crabs are producing a pustular surface, exit holes, scrape marks, discard pellets, and rosette structures, there also may be local occurrences of clots. Investigation of these show that crabs smaller than the mean size of the population are present as juvenile recruits that arrived later than the main population.

In the field there was a variability in behaviour. One group of crabs would emerge apparently *en masse* in one location on one day, and another group elsewhere which

remained in the subsurface on the first day, would emerge on another day. For any emergences, there would be a (usually small) proportion of crabs remaining in the subsurface. Emergent groups generally produced pustular structures before appearing on the surface. Further, on the third day, both groups may have produced pustular structures but had no emergences, then on the fourth day, both groups produced only pustular structures, but of a different plan shape. A third group may have remained subsurface for all four days, but emerged *en masse* in their resident location on the fifth day. In Figure 7, where the workings were mapped in detail in quadrats, there were no emergences on that particular low tide, but a local nearby emergence of crabs on the next day. Mapping of areas of pustular workings

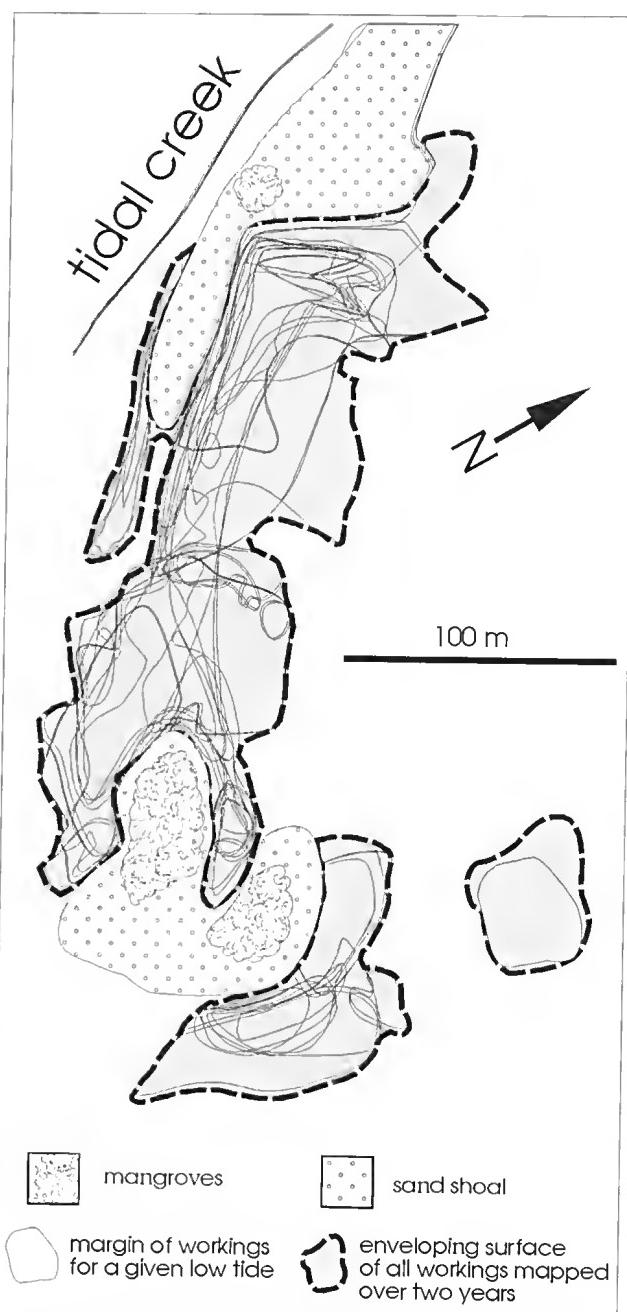


Figure 8. Map showing the overall distribution of the workings of crabs in southern King Bay over two years.

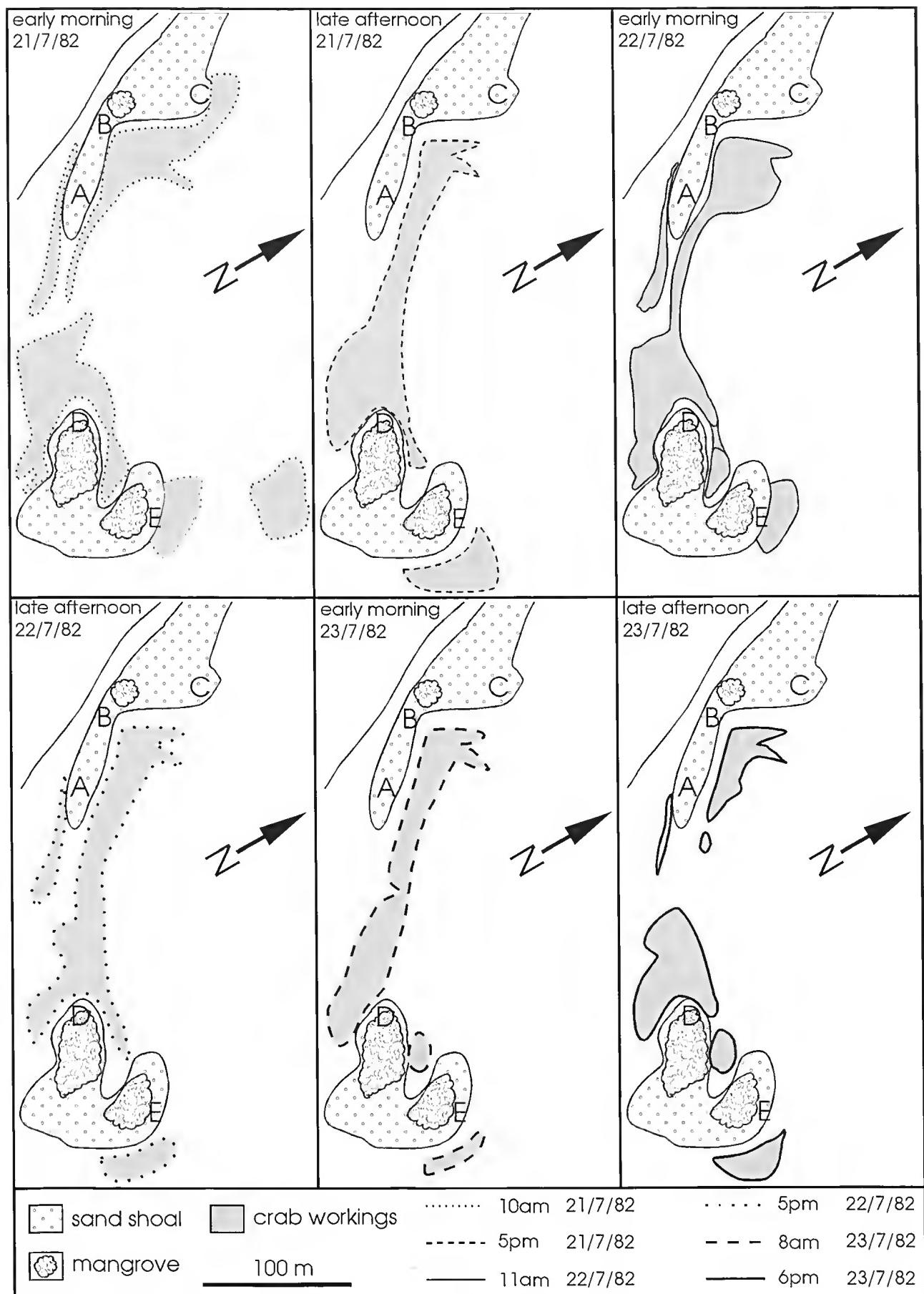


Figure 9. Maps of the workings of crabs in southern King Bay during six day-time low tides over three days.

shows that the boundaries of clusters of crabs within the large population resident within the habitat could change on a daily basis. Details of mapping are provided in Figures 8 and 9.

Figure 8 provides some background on the soldier crab habitat and the longevity of locations of crab activity as a prelude to describing the variability of soldier crab activity in this environment: there are some small mangrove coves inhabiting the crest of two tidal shoals that are part of the ebb-tidal fan in southern King Bay (Semeniuk & Wurm 1987). A distribution pattern of the soldier crabs, encompassing occurrences over two years (1981–1982) as determined by daily and monthly mapping, is shown in Figure 8; all mapped occurrences of the workings of the crabs are presented in this Figure, with an enveloping surface showing the maximum area that the crabs inhabited in southern King Bay. Soldier crabs had not inhabited the sites of the mangrove coves nor the upper parts of the sandy shoals above *circa* MSL. Their habitat preference here was the tidal flat between MSL and MLWN, along the margins of the shoal where the mud content is <5%, which approximately is parallel to topographic contours and to the crests of the shoals [the soldier crabs also generally had not inhabited the higher energy margins of the tidal creek, between MLWN and MSL, where tidal current flow and strong sediment mobility precludes their establishment]. As such, their overall distribution is circumferential to the shoals.

The distribution and variability of the crab workings over a three-day period with two tides a day are shown in Figure 9. For these three days, the crabs did not emerge, indicating that any variation in location of ichnological activity can not be the result of their emergence, migration, and then re-entry into the subsurface in new locations, hence generating a new location of ichnological activity. Without emergence, the variation of crab ichnological activity is the result of clusters or patches of crabs behaving variably in the subsurface from site to site. In detail, there is variability from tide to tide and from day to day, as will be described below. To facilitate description of the patterns, the two shoals are internally labelled as to their elongate spits and lobes as A, B, C, D and E.

On the morning low tide of 21st July 1982, the patches of crab workings occurred as thin strips projecting eastwards from either side of elongate spit A; the southern thin strip was absent during the afternoon low tide of the same day, reappeared on the morning and afternoon low tides of 22nd July 1982, was absent for the morning low tide of 23rd July, and was diminished in area for the afternoon low tide of 23rd July (Fig. 9). At the same time, crab workings appeared circumferential to the sand shoal lobe C on the morning low tide of 21st July 1982, but not again for the next five low tides. The re-entrant in the shoal (area B) showed crab workings that, while generally in the same location, expanded and contracted in area from day to day. Similarly, the sand shoal lobe of area D showed a fairly consistent circumferential occurrence of crab workings, but the detailed shape and the extent of the areas varied from low tide to ensuing low tides. The location north east of lobe E showed patches of crab workings that varied in occurrence and in shape, and in areal extent.

## Results from the aquarium

*Mictyris occidentalis* placed in the aquarium in the field and in the laboratory showed that these soldier crabs survived aquarium conditions. They grew from juvenile and sub-adult to fully adult while in the laboratory environment. The first experimental batch that was placed in the aquarium in the laboratory were sub-adult crabs initially and grew to be adults (with growth of mean carapace length from 5 mm to 14 mm) over nine months before they were released into the field at their place of capture. Figures 10–13 show the general results of the aquarium observations.

In the aquarium, the crabs carried out the same activities as they do in the natural environment. Their surface working and subsurface working activities occurred during the day-time and night-time. While they have been observed to emerge mainly during day-time low water, there have been some that emerged during night-time low water, as evidenced by their exit holes.

Whether in the sub-surface or emergent on the surface, the crabs inhabited the full length and width of the aquarium, producing ichnological structures across the whole sediment surface (Figures 10 and 11): meandering to linear, shallow surface-parallel tunnels; re-entry rosettes; and discard pellets (as will be described later). Fortunately, many of the 30 crabs also carried out their activities alongside the aquarium wall (with up to 10 at a time located along the aquarium wall), maintaining cavities, forming vertical to oblique back-filled burrows and creating the shallow surface-parallel tunnels, thus providing the opportunity to observe their activity in the subsurface. As such, there were direct observations of how crabs produce their ichnological structures which were useful for interpreting those in the field.

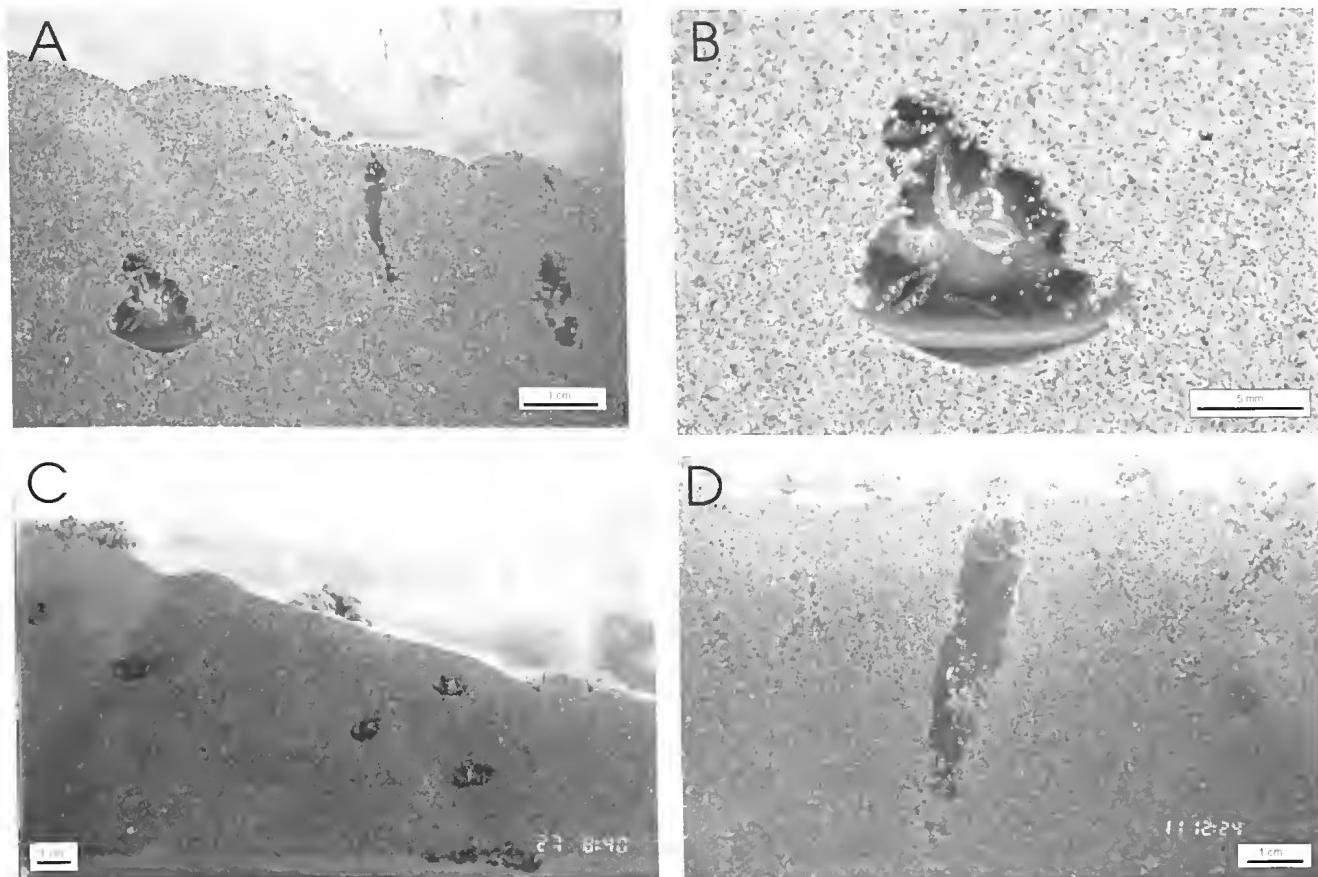
The first important observation of the aquarium conditions was that if tides were consistently mimicked, there was no emergence of crabs when the sediment was inundated at high water (simulating the high tide). The second important observation was that the crabs may continue their activity in the subsurface when the sediment was inundated on the high water.

The ichnological behaviour of the crabs is described in a framework of two water-level conditions:

1. that of high water, simulating high tide when sediments are inundated;
2. that of low water, simulating low tide with the water table at 20 cm to 5 cm below the sediment surface.

### Activities during high water

At high water, all crabs remained buried and produced cavities at depths of 5 cm to 15 cm, rarely to 20 cm (Figures 10A and 10B). These cavities essentially housed the crabs in an air-filled cavity that was *circa* 25% larger in diameter than the crab's size, and no crabs resided in the sand without being in such cavities. Within this cavity the crabs continually modified the wall of the open structure, so that over minutes to several hours the cavity slowly migrated vertically (upwards or downwards), or laterally (Fig. 13). In other words, the cavity was continually being modified and was migrating. Within the cavity, the crab maintained the air



**Figure 10.** Photographs of crab activities in the aquarium. A and B are of crabs when inundated. C and D are of crabs at low water. A. To left, crab in air-filled cavity with geopetal sludge on floor; to right, crab in another cavity; in the centre is a linear cavity; the sediment surface is comprised of former circular pustular structures that have collapsed with inundation. B. Close-up of (A) showing crab and geopetal sludge in cavity. C. Five crabs in cavities in the subsurface, and two circular pustular structures on the surface. D. Hollow shaft leading to an exit hole.

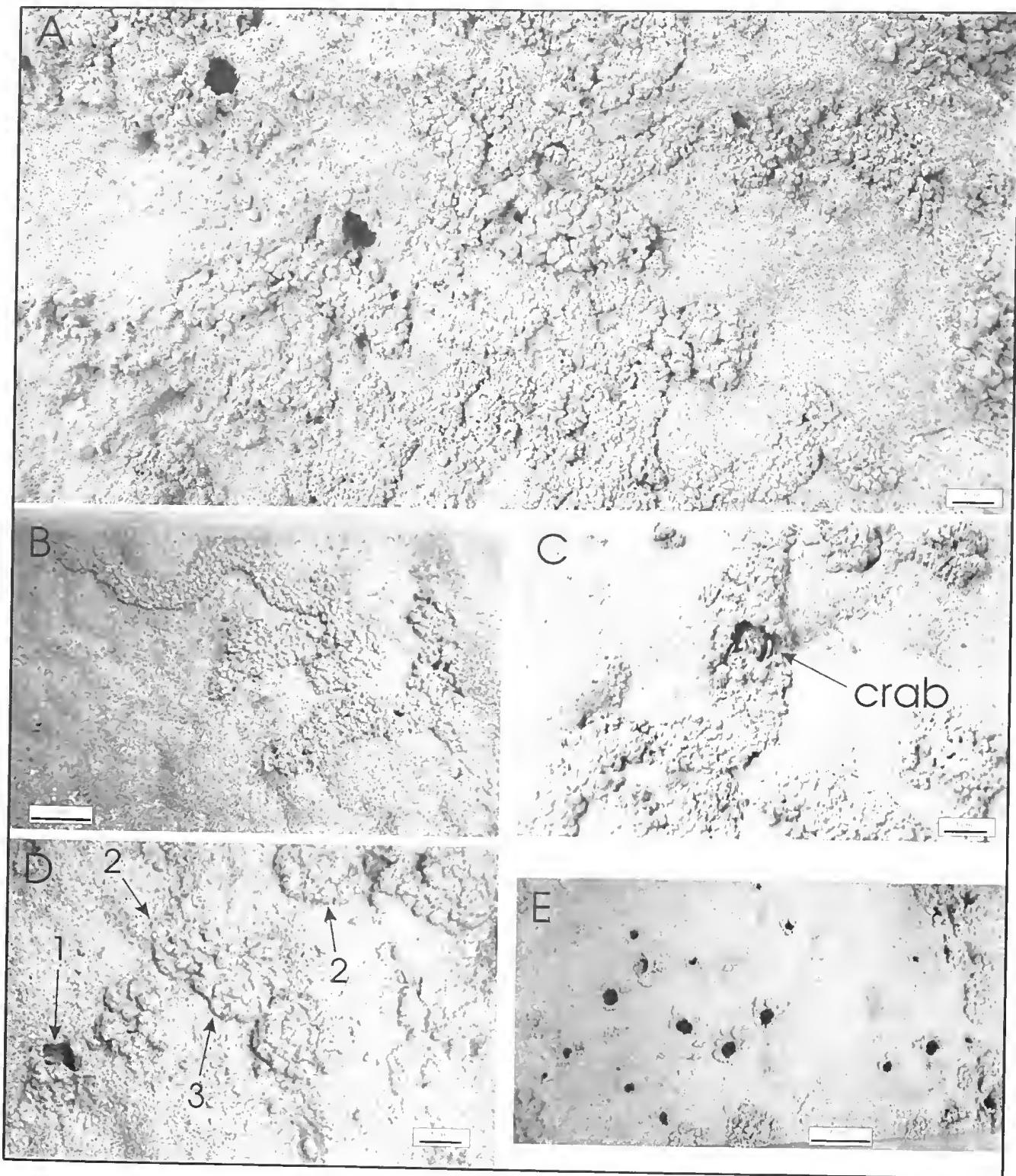
pocket and the ovoid cavity shape by employing the chelipeds and the first two pairs of walking legs to scoop or push the sand and the last two pairs of walking legs to act as stabilisers. Water seeped into the cavity creating on the floor of the cavity a pool of geopetal mud sludge <1 mm deep, up to 2 mm deep (Figures 10A and 10B). The crab, orientated in a dorsal surface upwards position, was feeding from this sludge, using its chelipeds and front walking legs in synchronous or alternating motions to scoop the muddy material into its buccal cavity. In this context, the feeding activity of the crab did not produce any discard pellets, and the crab directly utilised the muddy soup as feeding material. Occasionally the crab would scoop sand from the one side of the cavity and pack that material into its buccal cavity, then remain motionless for a short period except for lateral movements of the third maxillipeds. This material would be discarded as a semi-liquid unconsolidated mass and pushed to the opposite side of the cavity with outward sweeping motions of the chelipeds.

During intra-cavity activities such as feeding, cavity maintenance or migration, the crab appeared to attain inverted or lateral body orientations as well as the conventional dorsal surface upwards position with an equal facility.

Not all crabs were active at the one time. From a population of 30 crabs in the aquarium, a maximum of 10 were visible at any one time along the walls, and of these, activity was observed usually in 5 crabs at a time. During such times, the other crabs were under the sand in the interior of the aquarium and were not visible.

#### Activities during low water

During low water, a proportion of crabs emerged and some stayed subsurface. Those crabs along the aquarium walls provided the opportunity to document that even though the water table had fallen to below the level of a given cavity, and that while other crabs were constructing shallow surface-parallel tunnels or had emerged creating a hollow shaft and exit hole (Fig. 10D), some crabs remained in the subsurface in their cavities (Fig. 10C). Feeding motions of these crabs were the same as under conditions of high water except that there was no geopetal sludge in the bottom of the cavity and the material discarded from the buccal cavity was more cohesive but still not pellet-shaped as in surface discard pellets. Often these subsurface crabs remained relatively inactive. This inactivity may have lasted from minutes to hours, with the crab remaining motionless. When the aquarium was again inundated, these crabs returned to



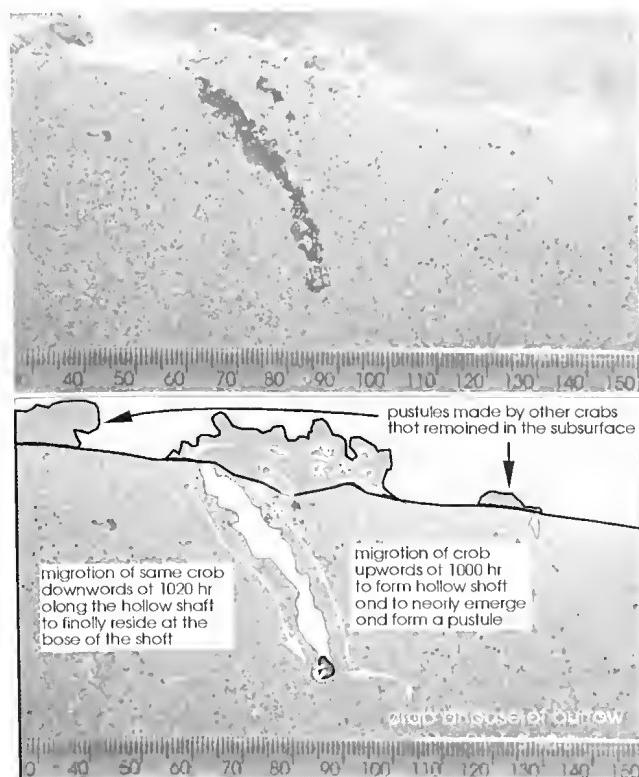
**Figure 11.** Photographs of crab activities in the aquarium during low water. A. Surface of aquarium sediment showing exit holes, eruption structures, circular pustular structures, meandering pustular structures, and rosettes. B. Meandering to linear pustular structures with crab in the tunnel exposed by an open roof. C. Eruption structure around an exit hole (arrow 1), rosettes (arrow 2), and circular pustular structures (arrow 3). E. Twenty exit holes, some with eruption structures, and several circular pustular structures.

their feeding and cavity-migrating activity, or still remained inactive.

Generally, whether during day-time or night-time, the activity of the crabs on the surface either in constructing shallow surface-parallel tunnels or emerging, was within 15–60 minutes of low water (the artificial low tide), and sometimes up to 150 minutes after the low water, though some crabs created circular pustules within minutes of low water (to re-excavate their cavity). The majority of crabs constructed shallow surface-parallel tunnels (Figures 11A, 11B and 11C). Those crabs active along the aquarium walls showed that the tunnel construction was achieved by creating discard pellets and attaching them to the roof of a developing tunnel, and by forming excavation pellets and also attaching them to the roof of a developing tunnel.

For a given period of low water, during the day-time low water periods, a minority of crabs usually emerged, and these formed exit holes with eruption margins. Where located along the aquarium wall, the exit holes commonly were the upper termination of a vertical to near-vertical hollow shaft showing that the crabs rapidly ascended the sand, then exited, leaving the hollow shaft in their wake rather than a back-filled structure (Figures 10D and 12). Sometimes, all the crabs in the aquarium emerged at the one time so that all 30 crabs were on the surface.

While on the surface, the crabs would feed, creating scrape marks and then discard pellets. Walking on the surface also created some dactyl prints. Eventually, the crabs re-entered the sediment in staggered intervals creating re-entry rosettes with a central plug.



**Figure 12.** Photograph and annotated tracing of aquarium wall showing the observed movement of one crab upwards and downwards within a hollow shaft. Scale in millimetres.

Again, for the low water activities, not all crabs were active at the one time. From the population of 30 crabs, a maximum of 10 were visible at any one time along the walls, and of these, activity was observed usually in 5–9 crabs at a time (Fig. 10C).

Figure 13 illustrates the variability of crab behaviour for six low water periods. The crabs variably emerged, or created pustular structures, or remained active or inactive in cavities, and their activities were not synchronised. Further, the mobility of individual crabs at the same time of observation varied temporally, and in terms of speed of their movement, direction(s) of their movements, and how far they moved.

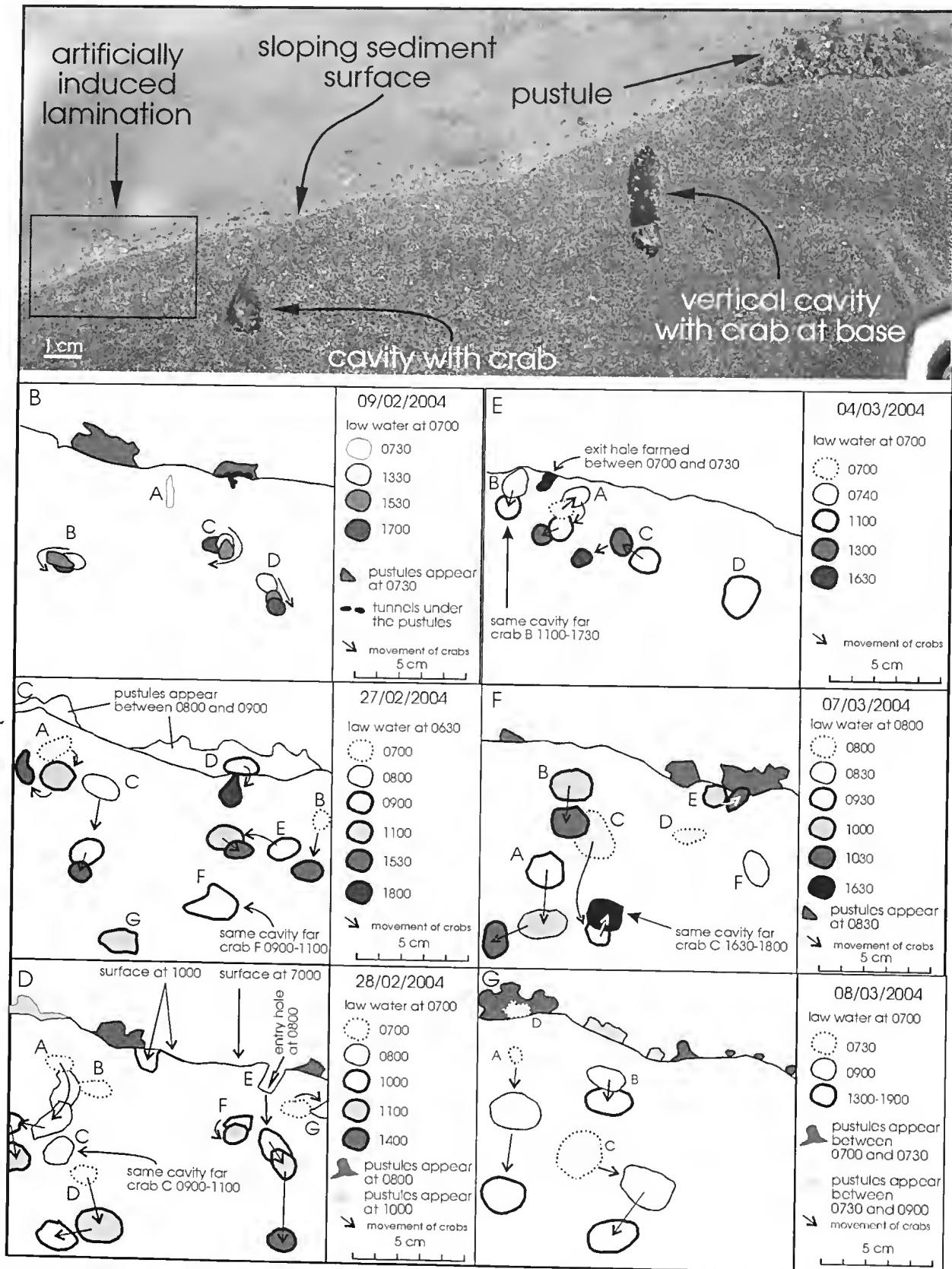
The activity of the crabs on the surface mimicked that in the field. Generally, immediately after the sediment surface was exposed at low water, the surface was devoid of ichnological structures. If the crabs remained in the subsurface, progressively in time, the surface of the sand was covered in circular pustules, or linear pustular structures (Fig. 11). If the crabs emerged, the surface initially was covered in circular pustules, or linear pustular structures by those crabs that remained in the subsurface or that were about to emerge, and was additionally, for those crabs that had emerged for a given low water episode, pocked with exit holes and covered with discard pellets and rosettes. The numbers of crabs that created pustular structures, or meandering pustular structures, or those that emerged to create exit holes, discard pellets, or rosettes, varied from low water period to low water period, from no emergences, to a maximum number of 30 (all of them).

An important aspect of the activity of the crabs in the aquarium was its variability:

1. during a given period of low water, not all crabs were active at the same time (where visible along the aquarium walls, some remained inactive in their cavities, some were active in their cavities, some excavated surface-parallel tunnels, and some emerged);
2. during another period of low water, most crabs might have been inactive at the same time, remaining in their cavities; i.e., there were no emergences and no development of pustular structures;
3. during another period of low water, all crabs appeared to be active at the same time, but some remained active in their cavities, some excavated surface-parallel tunnels, and some emerged; and
4. during yet another period of low water, all crabs emerged at the same time.

#### Subsurface sedimentary structures

The aquarium provided the opportunity to observe the movement of the crabs in the subsurface of the sediment and the sedimentary structures that were created as a consequence. Some of this description has already been provided above, but is re-iterated here in the context that there is a focus now on subsurface sedimentary structures of what are traditionally viewed as biogenic sedimentary structures rather than the surface ichnological features.



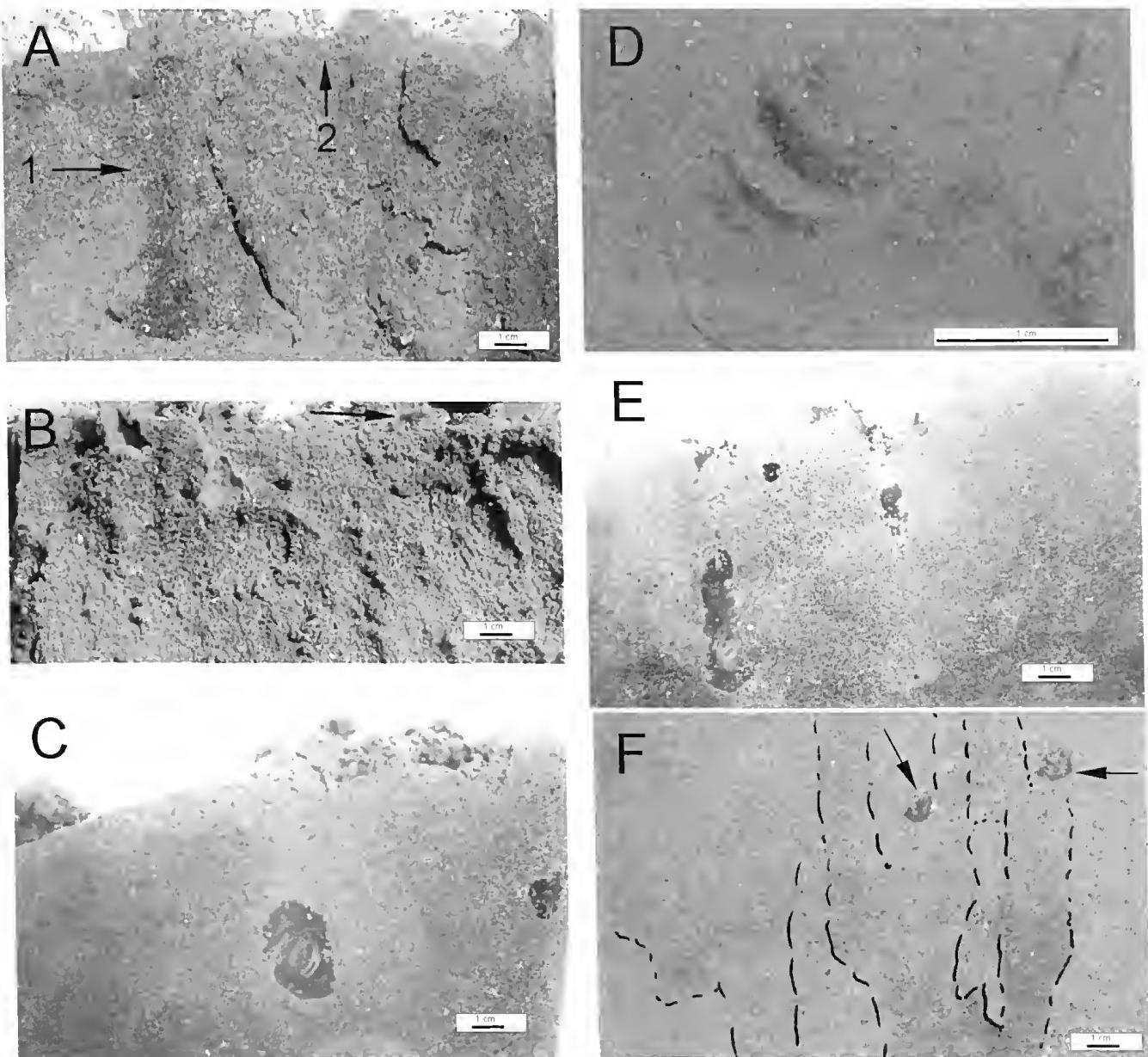
**Figure 13.** Results of the aquarium observations. A. Side view of the aquarium, one hour after low water, showing sloping sediment surface, pustule on surface, and two crabs in the subsurface, one in an equant cavity *circa* 2 cm below the surface, and the other in a vertical cavity located 1–4 cm below the surface. B–G. Tracings of the aquarium walls showing, for a given day, the number of crabs when they appeared, and the number and time that any crabs emerged. For a given frame, the crabs are notated A, B, C, D, etc. Since section: tangential sections appear as small cavities, and median sections show maximum size of a cavity.

The movement of the crabs in the subsurface is of two types:

1. vertical movement to rapidly emerge onto the sediment surface; this produces a vertical to near-vertical hollow shaft; and
2. lateral, vertical and downwards movement of the cavity; this produces a blurred bioturbation structure wherein the sediment appears swirled.

Where the sand was artificially laminated in the aquarium to trace the development of biogenic (bioturbation) structures, the process of burrowing and

cavity migration left a bioturbated zone of vertical corridors, swirls and mottled material in the upper 15 cm of the sediment (Fig. 14). Burrow back-filling and cavity wall modification by the crabs created a wall-parallel lamination that was highlighted by sand grainsize variation, fine mud lamination, and by iron-sulphide diagenesis (grain pigmentation). For example, movement of the crabs to the surface and to the subsurface via vertical hollow shafts ultimately resulted in the development of vertical to near-vertical bioturbation structures that were emphasised (highlighted) by diagenetic colouration (varying degrees of iron sulphide pigmentation).



**Figure 14.** Bioturbation structures generated by soldier crabs. A. Field photograph illustrating general mottled brown (oxidised) and grey (iron sulphide pigmented) sand, with vertical back-filled burrow structures (arrow 1), and surface oxidised zone (arrow 2). B. Field photograph illustrating general vertical back-filled burrow structures highlighted by brown and grey sand. The near-surface layers have cavities that have an oxidation halo. Pustular structure is on the surface (arrow). C. Photograph of aquarium wall showing crab in cavity, and vertical zone of bioturbation generated by this mobile crab, highlighted by brown and grey sand. D. Back-filled burrow, with back-filling highlighted by brown and grey sand. E. Crabs in equant and linear cavities, and general bioturbated (swirled) nature of the sediment (particularly evident in lower middle and lower right of the aquarium). F. Vertical back-filled structures highlighted by brown and grey sand; two crabs in their cavities are arrowed (margins of corridors of grey and brown sand outlined on aquarium wall).

## Summary of soldier crab ichnological products

The soldier crab *M. occidentalis* can produce up to 16 different types of ichnological products. These are the result of the crabs working the sediment at different stages of their life cycle, whether or not they emerge, and the working of the sediment at different times of the tide. The various ichnological products and a summary of their formative biogenic processes have been listed in Table 1 [note that components of integrated ichnological products are not treated as separate products, i.e., a tunnel floor is part of a tunnel, not a separate structure, and the term "workings" refers to the total aggregation of ichnological products that occur on tidal flats]. Most of the ichnological products are distinct and diagnostic of particular activities. Clots, craters, circular pustular structures, dactyl prints, the discrete discard pellets on the surface, eruption structures, exit holes, hollow shafts, linear pustular structures, rosettes, scrape marks, and surface-parallel tunnels exemplify this. However, the roofs of surface-parallel tunnels are composed of excavation pellets and discard pellets, and it has not been possible to macroscopically separate these after they have formed. Mat pustular structures are not the result of a separate activity but one of coalescence of other structures.

## Discussion and conclusions

Observations of soldier crabs in the aquarium were very useful because the crabs replicated activities observed in the field. In addition, the aquarium could be used for observations of crab behaviour not readily apparent in the field. Results from the first aquarium experiment in the field and subsequent laboratory experiments showed that soldier crabs rapidly became acclimatised to aquarium conditions, did not display aberrant behaviour after an initial settling-in period, and could survive for an extended time and grow to a larger than average size in aquarium conditions that replicated the temperature and tidal regime of their natural habitat. The aquarium also provided the opportunity to vary the environmental conditions to ascertain crab responses (as will be described in later papers).

For both field and aquarium situations, the initiation of surface activities by the crabs producing clots, pustules and linear to meandering to mat pustular structures was within 15–60 minutes of sediment exposure, when the sand was sufficiently dewatered, though we did notice that the aquarium crabs generally tended to initiate workings earlier.

Initially, while the results from field work emphasised the ichnological products on the sediment surface, and indeed the aquarium results reinforced and explained these phenomena, the aquarium observations provided insights into the behaviour of the crabs in the subsurface under simulated both high-tide and low-tide conditions. Knowledge that the crabs remain active under high-tide conditions is particularly important because the crabs spend more than 50% of their time under high tides, and previous to our laboratory observation it was not known what activities *M. occidentalis* carried out during times of inundation. The aquarium observations showed that

their burrowing, migration and feeding continues in the subsurface during inundation. Other tidal crabs from genera such as *Scopimera*, *Uca*, and *Ocypode*, which are generally surface feeders, clearly wait out the high tides in their burrows to re-emerge on the low tide (Hill & Hunter 1973; Crane 1975; Gherardi *et al.* 1999; Gherardi & Russo 2001). They then re-excavate their burrows, and undertake feeding on the surface during low tide (by creating feeding pellets, or by scraping diatom-rich material off the surface, or by scavenging detritus, respectively), to then re-bury themselves and wait out the next high tide in their burrows, safe from predators that invade their habitat on the flooding tide. Their specialised surface feeding activities do not continue into the subsurface. This study shows that the activities of the soldier crab take place during both high tide and low tide and hence can be a 24-hours-a-day exercise. Moreover, both the surface activities (during low tide) and subsurface activities (during low tide and high tide) involve feeding – the former, feeding from the surface sediment, resulting in the generation of discard pellets that form the roofs of the surface-parallel tunnels and in a surface litter of discard pellets, and the latter, feeding from the geopetal sludge flooring the cavities and from the sand of the cavity walls. The soldier crab, *M. occidentalis*, is a cryptic (in-faunal) animal, spending most of its life cycle as in-fauna, and, as such, in hindsight it was to be expected that it undertook its feeding activities in the subsurface during high and low tides.

There is a difference in strategy of feeding and products of feeding between low and high tide. Because at low tide the sand is cohesive with pellicular water, and this pellicular water largely is the only water available for the crab to slurry the fine-grained organic material in its buccal cavity for feeding. Thus *M. occidentalis*, during a low tide, in extracting pellicular water from the ball of sediment it has scraped up, produces cohesive discard pellets (on the surface or in the construction of the roofs of surface-parallel tunnels), leaving a (pellicular water depleted) discard pellet behind. Some species of *Mictyris* (*M. longicarpus*), while on the sediment surface, have been observed taking up water from surface pools which they then store internally and use for particle size separation in the feeding process (Dittmann 1996).

Sand generally cannot remain cohesive when it is water-saturated (Webster 1919; Carrigy 1970; Reineck & Singh 1980; Groger *et al.* 2003; Kleinhans & van Asch 2005; Nowak *et al.* 2005; Breien *et al.* 2007), unless it is held by an organic gelatinous matrix (cf. Bathurst 1967). Consequently, in order for the sand to remain cohesive as pellets, and to ensure that the roofs of the tunnels do not collapse, soldier crab activity that is manifest on the surface does not begin until the water content of the sand changes from being saturated to being pellicular. Thus, a determining factor for the development of a majority of the traces is cohesive sand with a film of pellicular water coating the sand grains, a feature that is conditional on the sand being exposed to the drying action of sun and wind some time after its exposure by a falling tide. Hence, soldier crabs do not work the sediment to create surface-parallel tunnels while the sand is under water. They also generally do not work the sediment to create surface-parallel tunnels in sediment recently exposed by

a falling tide. Similarly, the creation of discard pellets does not take place in water-saturated sand, but in sand that has pellicular water. The early onset of workings in the aquarium, as noted above, may be due to more rapid draining of interstitial water under aquarium conditions, resulting in the development of sand with pellicular water sooner than would occur under field conditions.

Because, the sand is not cohesive under high tides, *M. occidentalis* does not produce discard pellets during times of inundation. Rather, it directly utilises the water seeping into its air-pocket cavity, feeding directly on the sludge that accumulates on the cavity floor. We conclude that this sludge, in fact, is the material being extracted from the film of pellicular water that coats the sand grains when *M. occidentalis* is feeding at low tide. In the former situation (high tide), the crabs directly utilise fine-grained material that seeps into their feeding cavity. In the latter situation, the crabs harvest this film of sludge off the sand into their buccal cavity and leave behind a pellet of sand, depleted of fine-grained material and packed into a neat ball by their walking legs.

Discard pellets of *M. occidentalis* superficially appear similar to the feeding pellets of the sand bubbler crab *Scopimera* (in this case, in our observations in Western Australia, the sand bubbler crab is *Scopimera inflata*). However, there is a difference in arrangement of pellets and associated structures derived from feeding by *M. occidentalis* as compared to those derived by feeding by the sand bubbler crab. As described earlier, *M. occidentalis* emerges from an exit hole, and in its wanderings on the surface scrapes up sand, leaves scrape marks in isolation, moves away from the scrape site, and continues to gather sand until the ball of sediment is large enough to discard as a pellet. It deposits the discard pellet a short distance from the scrapings. The exit hole, the scrape marks and the discard pellets are in three unrelated locations. *S. inflata*, on the other hand, emerges from its burrow, and initially begins its foraging close to the burrow entrance. It scrapes up sand into a ball that rests on the sediment surface, and it gathers its food from the surface of the ball (the pellet). The pellet is bordered by scrape marks. Once the sediment is depleted of food, the crab moves a short distance in a radial line away from its burrow entrance and scrapes up more sand into a separate ball that rests on the sediment surface. This practice continues as the sand bubbler crab progressively moves further and further from the burrow entrance, leaving a line of pellets and scrape marks. In this case, the burrow entrance hole, the scrape marks and the feeding pellets are all locationally related.

In terms of burrow permanence, many crab species have fixed burrows (to which they return on the rising tide, as mentioned above), re-excavating or cleaning out their burrows on exposure at the next low tide, or have a permanent burrow entrance. Species of the fiddler crab *Uca* are an example of the former, and species of the ghost crab *Ocypode*, or the mangrove grapsid crabs are examples of the latter (Hill & Hunter 1973; Crane 1975; Gherardi *et al.* 1999; Gherardi & Russo 2001; Breitfuss *et al.* 2004). Other crabs, while adapted to shifting sand under wave and tidal action, or whose burrows collapse under water-saturated conditions, may re-establish their burrows in a single fixed position during the ensuing interval of the low tide. For example, species of the sand

bubbler crab *Scopimera* reside in a burrow that collapses at high tide (Gherardi *et al.* 1999). They re-excavate their burrows during low tide such that there is a permanent vertical burrow (whose entrance is surrounded by radiating rows of feeding pellets). The activities of *M. occidentalis* stand in contrast to the above. Their surface-parallel tunnels are ephemeral or transient structures, effectively similar to gastropods that forage and move through the sediment in the near-surface, creating a trail of ploughed sediment. The cavities of the soldier crabs also are generally ephemeral, transient structures, but can remain as a short term temporary (static) feature. In summary, the soldier crab, *M. occidentalis*, whether on the surface or in the subsurface, is generally mobile and, as such, creates a complex range of ichnological products that are ephemeral and transient. Our conclusion, therefore, is that the behaviour of *M. occidentalis*, in contrast to many other crabs, is ichnologically complex.

However, *M. occidentalis* is not alone in exhibiting such complex ichnological behaviour. Some degree of complexity, though not to the same level as *M. occidentalis*, was documented by Gherardi *et al.* (1999) for the Scopimerinae crab, *Dotilla fenestrata*. These authors related the variety of burrow-oriented activities of *D. fenestrata* to be the result of rigid and plastic patterns, essentially an adaptation to the vagaries of intertidal habitat. Gherardi *et al.* (1999) concluded that the activity of *D. fenestrata* could be classified in a number of stereotyped behavioural patterns, the occurrence of which may change throughout the low water or on the basis of the crabs' relative size, according to an expected schedule. Digging, for instance, was more pronounced in larger individuals and mostly occurred when the crab emerges or just before it seals itself inside the burrow at the flooding tide. However, in contrast, maintenance of their burrows was a constant behaviour. Gherardi *et al.* (1999) documented the range of adaptive flexible behaviour in *D. fenestrata*; this included: the presence within the same population of both burrow-centred crabs and wanderers; the construction by the burrow-centred crab sub-population of two types of burrows (feeding-trench burrows and igloos); and significant differences in the behavioural budgets of the inhabitants of the two burrows. The ability of this species to 'switch' modes of activity allows responses to both the predictable and unpredictable elements of intertidal environments. However, while there is relative complexity in behaviour of *D. fenestrata*, manifest to some degree in the abundance and types of its ichnological products, *M. occidentalis* appears to be a far more complicated crab in terms of its in-faunal or epi-faunal behaviour in relation to tides, its life stage, and its feeding strategies (whether emergent, in subsurface tunnels, or in subsurface cavities).

Our aquarium observations allowed us to identify that the creation of cavities is an important part of soldier crab activity, and this suggested a re-investigation of the crab in the field to find similar products of such activity. The details of the cavities in terms of their size, shape, and geopetal mud floors obtained from aquarium observations facilitated recognition of such features in the field, confirming that what was observed in the aquarium also was a feature of the natural tidal-flat environment (Fig. 6B).

Subsurface cavities formed by crabs have been documented by other authors (e.g., Cowles 1915), though they have ascribed different functions to them. Maitland (1986), for instance, in describing large membranous disks on the meral segments of *Scopimera* and *Dotilla*, considered that these crabs retreated on the high tide to an subsurface air chamber within which they continued to breathe air until the low tide. In effect, these subsurface cavities were considered by Maitland (1986) to be breathing chambers. We consider the cavities of *Mictyris occidentalis* to be a feeding chamber, a resting chamber, as well as a breathing chamber. In a study of the soldier crab, *Mictyris longicarpus*, from Eastern Australia, Maitland & Maitland (1992) concluded that the species is an obligate air-breather. Their gill chambers were modified for both water circulation and air-breathing in that water circulates through lower gill compartments, and upper regions of the gills are air-filled, functioning as lungs. This duality of function of the breathing chambers enables the crabs to operate on the surface, explains their need for an air-pocket in the subsurface at high tide, and how they survive if the air-pocket collapses. From aquarium observations, Maitland & Maitland (1992) also describe *Mictyris longicarpus* as constructing an "igloo" (or domed sand roof) above a pocket of air at the sediment surface prior to flooding by the tide, and then descending, with the pocket of air, to 10–30 cm depth, to wait out the high tide [this "igloo" is analogous to the rosette structures described for *Mictyris occidentalis* in this paper]. In this respect, the behaviour of *Mictyris longicarpus* overlaps with *Mictyris occidentalis* of this study. In another paper, Takeda *et al.* (1996) described "igloo" construction in the ocyopodid crab *Dotilla myctiroides*. In addition to constructing its vertical burrow, *Dotilla myctiroides* rotates in the sand to form a circular wall of sand pellets around it and subsequently roofs the wall with pellets (the domed sand roof mentioned above). The resulting burrow structure, also termed an "igloo" by Takeda *et al.* (1996), encloses a small quantity of air together with the crab itself. Takeda *et al.* (1996) considered that such air chambers greatly facilitated vertical movement of the crab, and that the making of an "igloo" was an adaptation to enable construction of an air chamber in semi-fluid sand, where vertical burrows cannot be constructed, because the sand was not sufficiently firm to prevent collapse. Again, in contrast, we consider the cavities of *Mictyris occidentalis* to be a feeding chamber, a resting chamber, and a breathing chamber, regardless of the consistency of the sand. Takeda & Murai (2004) also documented *Mictyris brevidactylus*, a soldier crab from Southeast Asia, constructing two types of air chambers, one near-surface for feeding, and the another, a deeper ovoid form for residency. In this context, *Mictyris brevidactylus* appears to be constructing surface-parallel tunnels and subsurface cavities, similar to *Mictyris occidentalis*.

Discovery of distinctive subsurface bioturbation structures evident in aquarium studies also directed us to revisit the field environment to investigate and focus on similar structures in the sediment. The characteristics of bioturbation structures meant that *M. occidentalis*, in addition to its other obvious ichnological structures, left diagnostic subsurface structures in the sand, that (if all other ichnological products were to be erased by processes such as wave action or cavity collapse) could

remain as a signature of the former presence of these crab (Fig. 14).

An important conclusion to emerge from this study was that the ichnological products of the soldier crab relate to the life stage of the species, to whether or nor the adult crab emerged, and to the tides. There are three periods of ichnological products related to life stages of the crabs. Populations dominated by crabs in their settlement phase and early stage of their life cycle develop sediment surfaces strewn with clots. Populations dominated by crabs in the early to middle stages of their life cycle develop sediment surfaces covered in pustular structures, and concomitantly create subsurface cavities. Populations dominated by crabs in the middle to late stage of their life cycle develop sediment surfaces covered in pustular structures, cavities in the subsurface, exit holes, (sometimes) dactyl prints, discard pellets, and rosettes. Mixed-sized populations resulting from continuous or pulsed juvenile recruitment into the population therefore create a mix of ichnological products.

The observation of variability in behaviour in the crab population in the aquarium had direct implications to interpreting the activity of crabs in the field where there was also variability in behaviour. The aquarium observations confirmed that the crabs did not always behave consistently as similar units. There was consistency in crab behaviour in that they built the same types of structures at the same time of tide: e.g., pustular structures were produced on the low tide; exit holes, the formation of discard pellets, and rosettes also were produced only on the low tide. The development of cavities occurred on low and high tides. But outside of these patterns specific to the whole species, the crabs appeared to have independent behaviour. Thus, while there may have been emergences *en masse*, or large areas worked into pustular surfaces, it was not predictable that all crabs would all emerge throughout the entire habitat at the same time, and that all crabs in the subsurface worked the sediment to create a pustular surface, or that all crabs in the subsurface worked in their cavities at the same time. Rather, the emergences and development of pustular surfaces, and the periods of quiescence of surface activity was variable from site to site in the habitat (measured in terms of several metres), even though the entire habitat (measured in terms of several tens of metres to hundred of metres) was populated by these crabs in the subsurface. The variability of behaviour of the crabs in the aquarium could have been interpreted as an aberration or artifact of the behaviour of crabs imprisoned in a tank, but in fact, once the factor of behavioural variability was determined, it correlated with observation of crab behaviour in the field, and explained observations of the behaviour of natural crab populations in our studies over decades. That is, the behaviour of the crabs in the natural environment has similarly been sporadic or variable. In contrast, *Scopimera* and species of *Uca* in a given burrowing population generally all behave similarly at the same time (there are generally no absentees or deviations from the individual pattern, so if one crab emerges and feeds, then all crabs appear to emerge and feed). But soldier crabs are variable in behaviour: under the same conditions of exposure, light, wind, pellicular water

content, and salinity, not all individuals act the same way; some emerge, some tunnel, some stay in the subsurface; then the next day all may emerge; and for the ensuing days the variable behaviour continues. This was particularly emphasised by the aquarium studies because clearly all external factors of exposure, light, wind, pellicular water content, and salinity were similar throughout the aquarium, yet individuals in the population of 30 crabs did not respond uniformly.

The variability of preservation of soldier crab ichnological products also relates to the tidal cycle, i.e., whether it is a period of spring tide or neap tide. Spring tides are associated with more swift tidal current velocities, and crab ichnological products have a higher chance of reworking during an ensuing high tide. During neap tides, with the thin film of mud deposited by scour lag / settling lag processes, soldier crab ichnological products stand out in contrast, and have the best chance of preservation; also, dactyl prints and tracks, if present, are best preserved on the mud films.

In summary, the key points deriving from aquarium observations of crab activity below the sediment surface was that there were cavities, that crabs were feeding from sludge at the base of the cavity, that there was subsurface movement of the crabs, (laterally and vertically, and similar movement, axiomatically, of the cavity around them), that vertical hollow shafts were produced by a crab in the process of emerging and re-entering the sediment, and that the subsurface activity could produce distinctive bioturbation patterns. There was a range of ichnological products generated by the same organism depending on stage of life, time of tide, and whether the crab emerged or not.

The key soldier crab traces, in chronological order of development from time of high tide to time of low tide, are: cavities, clots, excavation pellets and discard pellets, meandering pustular-sand-roofed surface-parallel tunnels, exit holes, dactyl prints, scrape marks, surface-deposited discard pellets, and rosettes. The discard pellets forming the tunnel roof and the surface discard pellets are formed the same way, but one is attached by the crab to the roof from below, the other is formed on the surface by emergent crabs, albeit the latter contain more pellicular water and are initially less cohesive, and are also more pigmented.

Our study showed a direct correlation between field work and aquarium observations, and provided explanation of the field results. All ichnological products observed in the aquarium had their counterpart in the natural environment. Interestingly, while the aquarium study was set up to observe and explain what was documented in the field, and to add to our understanding of the ichnological behaviour of the crabs, it resulted in the observation of additional features such as mud-floored cavities and bioturbation structures that initially were not readily apparent or interpretable in the field, and that now could be targeted specifically for discovery and investigation in the field.

The ichnological results of the paper also can be useful paleoichnologically in Quaternary rocks for the identification of soldier crab workings and interpretation of tidal environments that soldier crabs inhabit.

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# A new GPS-based evaluation of distortions in the Australian Height Datum in Western Australia

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## Abstract

Previous work on assessing the errors in the Australian Height Datum (AHD) across Western Australia used fewer and older global positioning system (GPS) data and a global quasigeoid model. A larger and improved State-wide set of 243 GPS-derived ellipsoidal heights and a regional gravimetric quasigeoid model are now available. Therefore, it is possible to re-evaluate the north-south tilt in the AHD and look for regional systematic distortions with some more confidence in Western Australia. This new analysis shows an apparent north-south tilt of ~0.27 mm/km in the existing AHD over the whole of the State, but which increases to ~0.6 mm/km over smaller regions, showing regional systematic distortions. When mean sea-level constraints are removed from the AHD by a minimally constrained least-squares adjustment of the spirit-levelling observations that is less prone to the effect of sea-surface topography, the north-south tilt reduces to ~0.18 mm/km, but the regional distortions remain, showing that errors are present in the spirit-levelling observations.

**Keywords:** Heights, geodesy, GPS, quasigeoid, AHD, levelling, sea surface topography

## Introduction and Background

Featherstone and Stewart (1998) first suggested the presence of distortions in the Australian Height Datum (AHD) across Western Australia (WA) based on Global Positioning System (GPS) and quasigeoid data from a global model. However, their analysis used a reasonably old (1996) GPS dataset of 63 points and the EGM96 global quasigeoid model (Lemoine *et al.*, 1998). The spatial resolution of EGM96 is only ~55 km. Later, Featherstone (2004) used a 2002-observed GPS dataset of 48 points (Featherstone *et al.*, 2004) and the AUSGeoid98 regional gravimetric quasigeoid model (Featherstone *et al.*, 2001) to indicate a north-south tilt of ~0.81 mm/km in the AHD, but only over part of south-western WA. The spatial resolution of AUSGeoid98 is ~4 km through the addition of regional gravity and terrain data in a modified Stokes integral (cf. Featherstone, 1999).

The study reported here uses a larger and improved (through more sophisticated processing techniques and models) WA-wide GPS dataset of 243 points and a modified version of AUSGeoid98 to look for a north-south-tilt in the AHD (cf. Featherstone, 2004; 2006), as well as for higher-order distortions (cf. Featherstone and Stewart, 1998). The modified version of AUSGeoid98 used was ‘augmented’ (Featherstone, 2007) using gravity field data from the Gravity Recovery And Climate Experiment (GRACE) satellite mission (e.g., Tapley *et al.*, 2004). As such, this quasigeoid model is expected to be less prone to long- and medium-wavelength errors, thus strengthening its power to detect distortions in the AHD.

## Methods, Data and Results

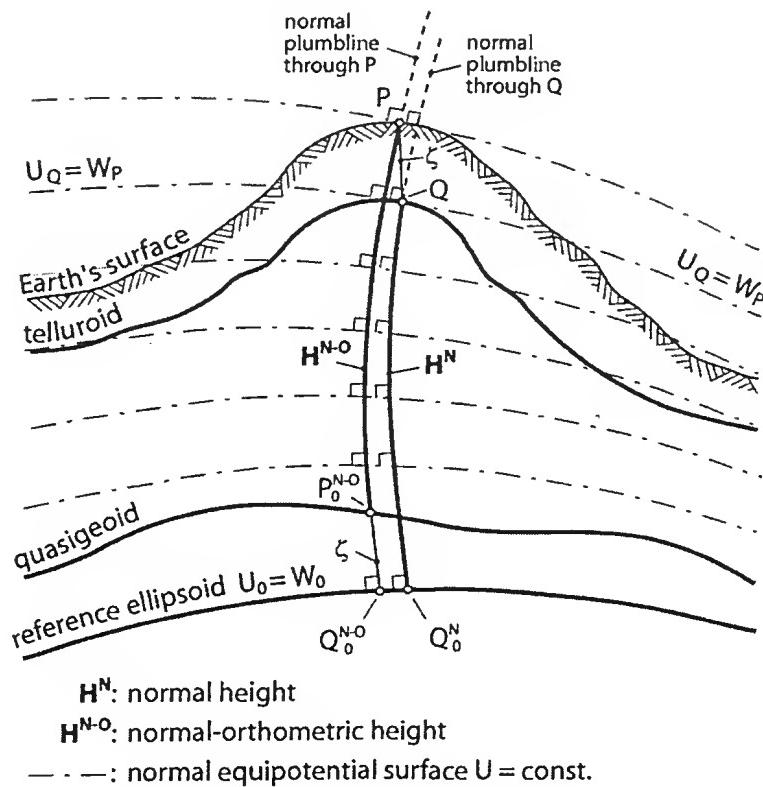
Errors in the AHD ( $\varepsilon$ ) can be assessed using GPS and a quasigeoid model via:

$$\varepsilon = h - \zeta - H_N \quad (1)$$

where  $h$  is the GPS-derived ellipsoidal height,  $\zeta$  is the gravimetric quasigeoid height (cf. Featherstone *et al.*, 2001; Featherstone, 1999, 2007), and  $H_N$  is the spirit-levelled AHD height (cf. Roelse *et al.*, 1975). All quantities must refer to the same ground point.

The AHD uses the normal-orthometric height system (e.g., Roelse *et al.*, 1975; Heck, 2005; Featherstone and Kuhn, 2006), which is the distance measured along the normal gravity plumbline from the quasigeoid to the point of interest (Figure 1). The advantage over other types of heights (e.g., orthometric or normal) is that it does not require gravity observations along the levelling traverses, which are typically not available in Australia. However, AHD heights are not fully normal-orthometric because they were derived from a cumulative correction to levelled height differences for the GRS67 ellipsoid (IAG 1967) using a truncated form of Rapp’s (1961) formulas (Roelse *et al.*, 1975).

The 243 GPS-derived ellipsoidal heights used in this study came from a GPS SINEX (system independent exchange format) file created by the WA geodetic agency, Landgate, comprising most of its geodetic-quality GPS data archives (L. Morgan, 2007, pers. comm.). The term ‘geodetic-quality’ means dual-frequency carrier-phase GPS data collected continuously for at least six hours at each point. These data were processed by Hu (2007, unpublished) using the Bernese v5 scientific GPS analysis software (Hugentobler *et al.*, 2006) and products from the International GNSS Service (Moore and Neilan, 2005).



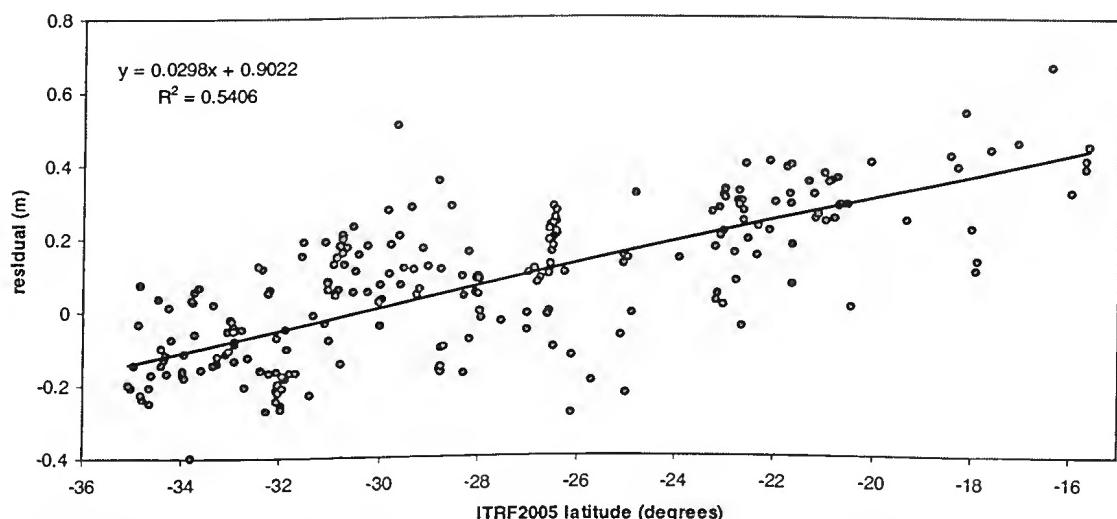
**Figure 1.** The normal-orthometric height  $H^{NO}$  is reckoned along the normal gravity plumblne from the point on the quasigeoid to the point  $P_0^{NO}$  on the Earth's surface. The quasigeoid height  $\zeta$  is reckoned along the ellipsoidal surface normal from point  $Q_0^{NO}$  on the ellipsoid to point on the quasigeoid. The ellipsoidal height  $h$  is reckoned along the ellipsoidal surface normal from the surface of the ellipsoid to the point  $P_0^N$  on the Earth's surface (from Featherstone and Kuhn, 2006).

All GPS-derived ellipsoidal heights are in terms of the latest ITRF2005 reference frame (Altamimi *et al.*, 2007) and expressed relative to the surface of the GRS80 reference ellipsoid (Moritz, 1980).

The officially published AHD heights, derived from mainly class-C (ICSM, 2002) sprit-leveelling observations, were also provided by Landgate (L. Morgan, 2007, pers. comm.). The GRACE-augmented version of AUSGeoid98

(Featherstone, 2007) was bi-cubically interpolated to the GPS positions using the software in Featherstone (2001).

The advancement offered by this study over previous GPS-quasigeoid-based studies on the AHD (Featherstone and Stewart, 1998; Featherstone *et al.*, 2001; Featherstone and Guo, 2001; Featherstone, 2004, 2006; Baran *et al.*, 2006) is the use of more, better spaced (cf. Figures 3 and 7) and reprocessed GPS data (Hu, 2007, unpublished),



**Figure 2.** Linear regression of the GPS-quasigeoid-AHD residuals ( $\epsilon$ ) in metres versus latitude in degrees. From the gradient in degrees, this gives an apparent tilt of  $\sim 0.27$  mm/km.

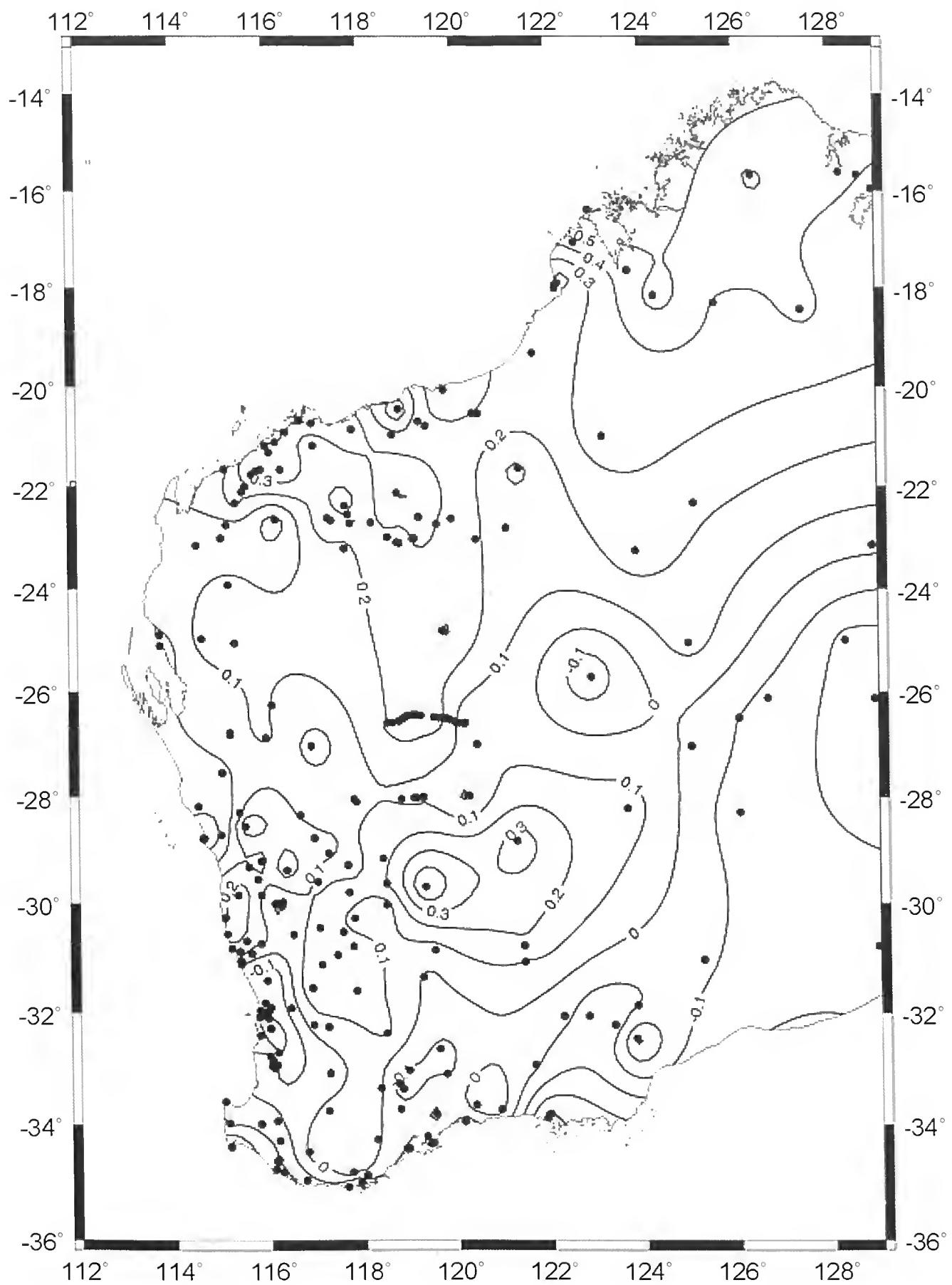


Figure 3. Contour plot (in metres) of the GPS-quasigeoid-AHD residuals ( $\epsilon$ ) and the 234 GPS-AHD points (Mercator projection)

and the GRACE-augmented AUSGeoid98 (Featherstone, 2007).

The average of the one-sigma precision (*i.e.*, standard deviation) of the 243 GPS-derived ellipsoidal heights is ~2 mm, which comes from internal error propagation in the Bernese software (Hu, 2007, unpublished). However, internally propagated GPS errors are typically overoptimistic by an order of magnitude, so ~20 mm is a more reasonable error estimate for these data. The precision of the GRACE-augmented AUSGeoid98 is much harder to estimate. Indeed, no-one has yet come up with the full error-propagation formulas for regional gravimetric quasigeoid models. Therefore, it is cautiously estimated to be ~100–200 mm, but this value remains open to debate.

Some other *caveat emptors* are necessary before presentation and discussion of the results. Distortions in GPS-derived ellipsoidal heights have never been reported, and the precision estimates for the data used here are all consistently around the same level and not spatially correlated. As such, this is the most reliable data source used here. On the other hand, it is impossible to reliably isolate what proportion of the residuals  $\varepsilon$  comes from the quasigeoid model or from the AHD; the so-called inseparability problem (Featherstone, 2004). This creates a problem when trying to correctly attribute the residuals  $\varepsilon$  solely to tilts and distortions in the AHD, but this will be circumvented in part by also using readjusted spirit-levelling heights (described later).

#### **Results for official AHD heights in WA**

To look for latitudinal (north-south) and longitudinal (east-west) trends in the residuals  $\varepsilon$  (Eq. 1), and particularly for a north-south tilt in the AHD across WA, we performed linear regressions in latitude (Figure 2) and longitude (Figure 4).

A north-south apparent tilt is shown in Figure 2, which is reasonably significant with an  $R^2$  value of ~0.54. This tilt is equivalent to ~0.27 mm/km when converting degrees to kilometres (one degree is ~111 km at the equator), which is less than the value of ~0.81 mm/km determined in southwest WA (Featherstone, 2004). This indicates further higher-order distortions in the AHD, where apparent tilts will be different in different regions. Indeed, this is seen from Figure 2, where a linear regression of the residuals  $\varepsilon$  south of ~29°S latitude, which includes the area studied by Featherstone (2004), would give a larger tilt of ~0.60 mm/km.

These non-linear distortions are mapped in Figure 3 using tensioned spline interpolation from the Generic Mapping Tools (Wessel and Smith, 1998; <http://gmt.soest.hawaii.edu/>), together with the locations of the 243 GPS-AHD points. Most of the high and low contours of the residuals  $\varepsilon$  correlate spatially with those in Featherstone and Stewart (1998). The largest residuals are persistent in the western Goldfields region (centred at ~30°S, ~120°E) and in the northern Kimberley region (centred at ~16°S, ~126°E). As will be shown later, these are most probably due to spirit-levelling errors. The north-south trend (*cf.* Figure 2) is due to the constants applied to the AHD, which are described later.

Contrary to expectation based on previous studies (Featherstone and Stewart, 1998; Featherstone *et al.*, 2001;

Featherstone and Guo, 2001; Featherstone, 2004; 2006; Baran *et al.*, 2006), there is a small east-west tilt of ~0.07 mm/km in Figure 4, but it is not statistically significant with an  $R^2$  value of ~0.02; there is a large longitudinal scatter in the residuals. Again, this indicates distortions in the AHD, but is less reliably determined than the north-south trend in Figure 2.

#### **Results for unofficial heights in WA**

Next, we sought the source of the above distortions in the AHD in WA using another set of normal-orthometric heights. A large proportion of the north-south tilt in the AHD has been previously attributed to sea-surface topography (SST) effects (*e.g.*, Featherstone, 2001; Featherstone and Kuhn, 2006). This is because mean sea-level (MSL) was fixed to zero height at 30 tide-gauges to realise the AHD on the mainland, and the distorting effect of this approach was recognised at the time (Roelse *et al.*, 1975). SST is the difference between the geoid and MSL, caused by ocean currents and other oceanographic phenomena (*e.g.*, Pugh, 1987).

Around Australia, SST is dominantly north-south-trending (*e.g.*, Tapley *et al.*, 2003), so gives the most plausible explanation for the north-south tilt in the AHD observed in Figures 2 and 3. However, the east-west tilt in the AHD observed in Figure 4, albeit less significant, is enigmatic. One factor could be the presence of the Leeuwin Current, which is a narrow (~50 km), long (~5500 km) and meandering coastal eastern boundary current along the Australian continental shelf slope. It moves southward west of WA's coast, then heads eastwards into the Great Australian Bight south of WA, and finally to the southern tip of Tasmania (Ridgway and Condie, 2004). Such boundary currents will cause near-coastal SST effects, so could account for some of the east-west apparent tilt.

In order to determine the SST contribution to the apparent tilts and distortions in the AHD, we least-squares adjusted the normal-orthometric spirit-levelling observations used to establish the AHD without the effects of SST. These spirit-levelling data were supplied by the national geodetic agency, Geoscience Australia (G. Johnston, 2006, pers. comm.). We performed a minimally constrained adjustment (*i.e.*, by fixing only one tide-gauge at Albany) of these spirit-levelling data to determine new normal-orthometric heights for the 243 GPS stations, and then repeated the earlier experiments using these spirit-levelled heights that are uncontaminated by SST. SST at Albany will still affect these readjusted heights, but this is a constant value that will not affect the identification of tilts and higher order distortions, so is unimportant.

This second analysis will indicate how much the MSL constraints cause the apparent tilts and distortions in the AHD. Ten tide-gauges were held fixed to zero height at MSL in the original AHD around WA (Roelse *et al.*, 1975); Eucla, Esperance, Albany, Bunbury, Fremantle, Geraldton, Carnarvon, Port Hedland, Broome and Wyndham).

Figure 5 is equivalent to Figure 2 and Figure 6 is equivalent to Figure 4, but now use heights from the minimally constrained least-squares adjusted spirit-levelling observations without SST contamination. These

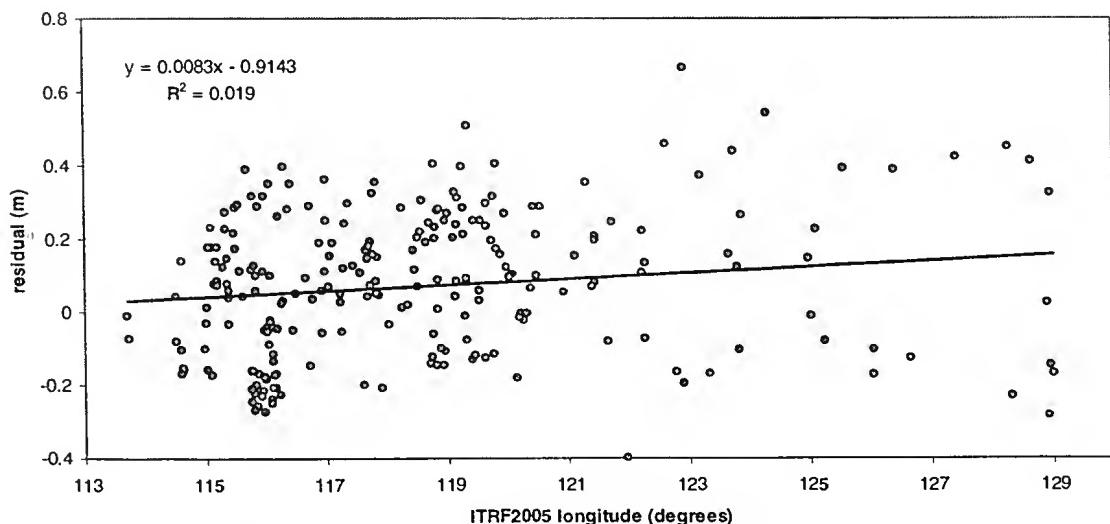


Figure 4. Linear regression of the GPS-quasigeoid-AHD residuals ( $\epsilon$ ) in metres versus longitude in degrees. From the gradient in degrees, this gives an apparent tilt of  $\sim 0.07$  mm/km.

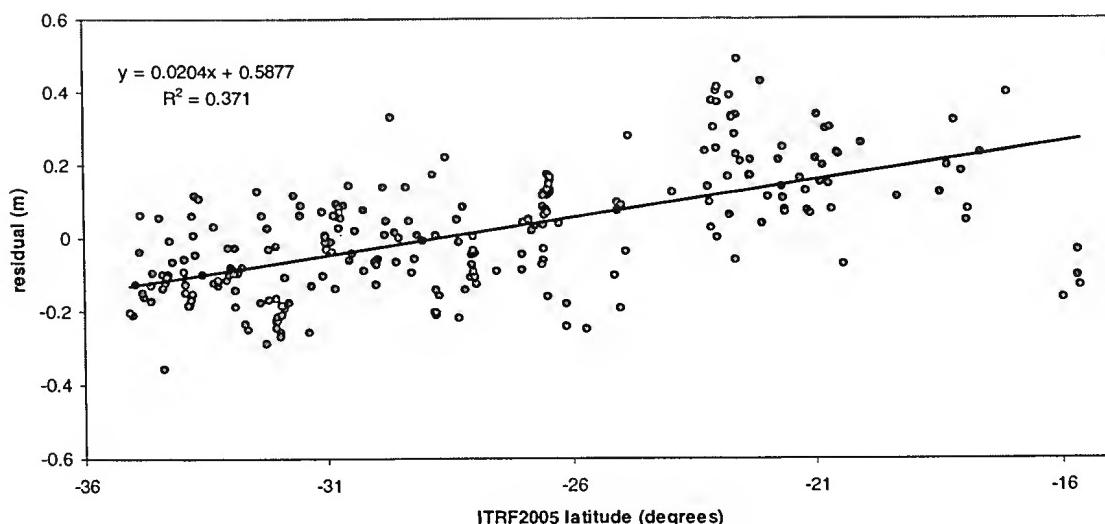


Figure 5. Linear regression of the GPS-quasigeoid-AHDnoSST residuals ( $\epsilon$ ) in metres versus latitude in degrees. From the gradient in degrees, this gives a tilt of  $\sim 0.18$  mm/km.

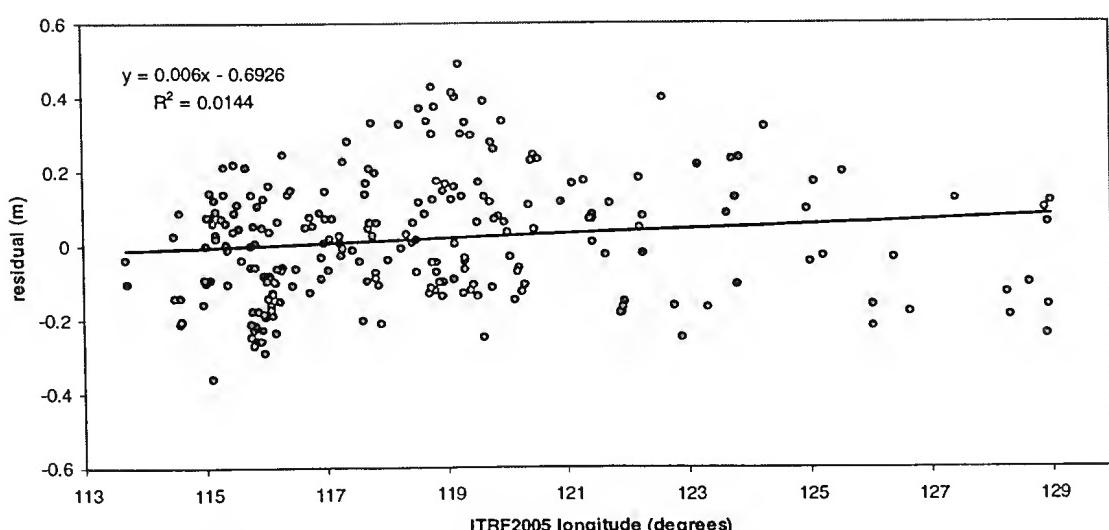


Figure 6. Linear regression of the GPS-quasigeoid-AHDnoSST residuals ( $\epsilon$ ) in metres versus longitude in degrees. From the gradient in degrees, this gives a tilt of  $\sim 0.01$  mm/km.

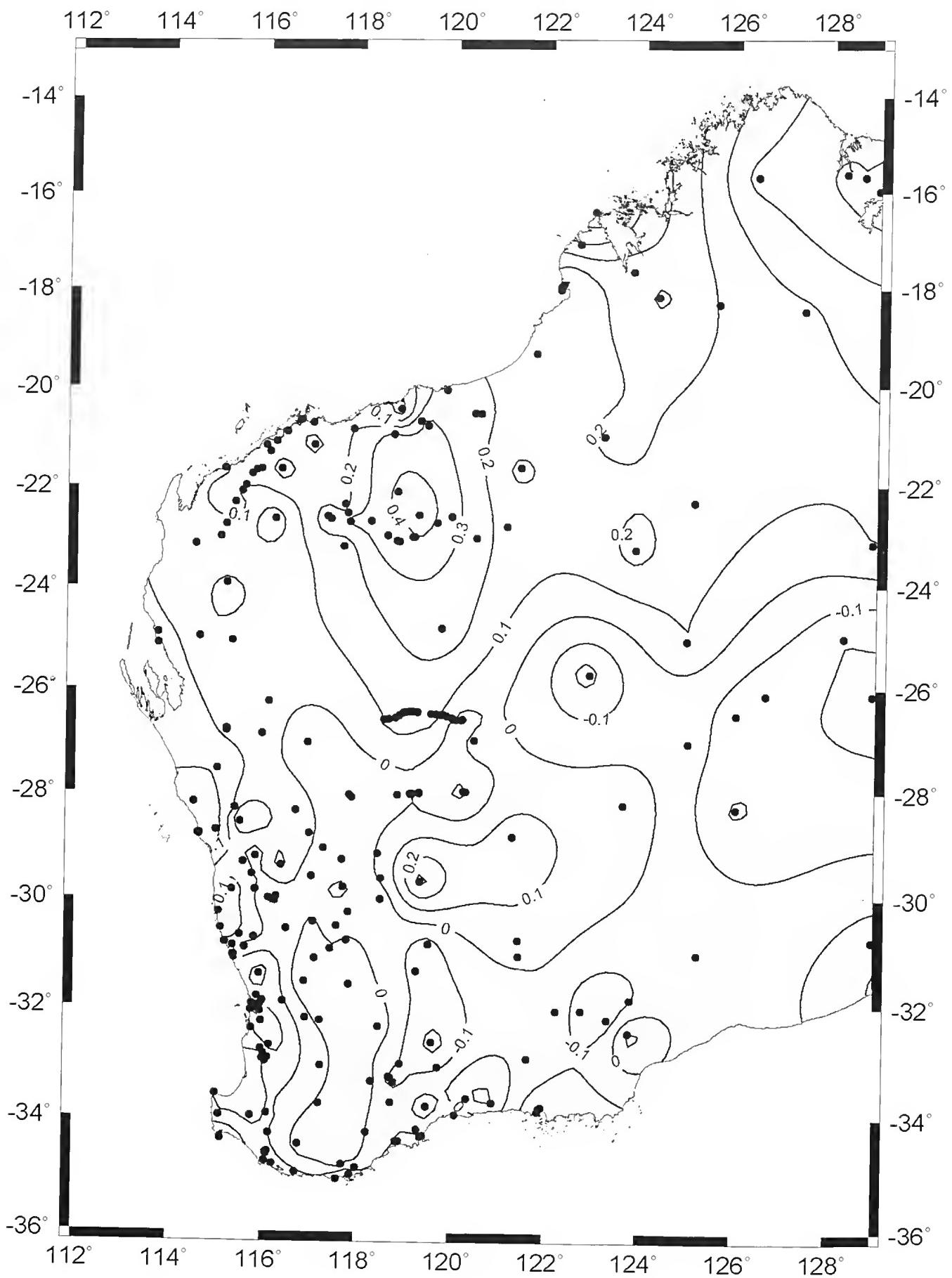


Figure 7. Contour plot (in metres) of the GPS-quasigeoid-AHDnoSST residuals ( $\epsilon$ ) and the 234 GPS-AHD points (Mercator projection)

**Table 1**Descriptive statistics of the residuals ( $\varepsilon$ ) in metres

Residual	Maximum	Minimum	Mean	STD
GPS-quasigeoid-AHD	0.666	-0.437	0.071	$\pm 0.203$
GPS-quasigeoid-AHDnoSST	0.606	-0.359	0.018	$\pm 0.168$
"				

readjusted and SST-free height data will be termed AHDnoSST to distinguish them from the officially published AHD heights used earlier.

The contour plot in Figure 7, compared to Figure 3, confirms that the residuals  $\varepsilon$  have been reduced in magnitude after the minimally constrained readjustment of the spirit-levelling observations without the SST-affected constraints used to realise the official AHD. However, parts of the general pattern in Figure 3 remain (notably in the western Goldfields and northern Kimberley), though the magnitudes are reduced. This strongly suggests that the spirit-levelling observations are the cause of the regional distortions, but the SST effects on the constrained AHD adjustment also act to exacerbate them.

Table 1 summarises the descriptive statistics of the residuals  $\varepsilon$  for the 'official' AHD heights and 'unofficial' readjusted (AHDnoSST) heights that are not affected by SST constraints. The summary by descriptive statistics is permitted because the residuals are reasonably normally distributed. First, the mean values should be neglected because of the unimportant 53 mm constant bias caused by the SST at Albany. The range (maximum minus minimum) is reduced by 138 mm when the SST constraints are removed, and the standard deviation decreases by 35 mm. Therefore, SST accounts for a reasonable proportion of the larger residuals in Figures 2 to 4 versus Figures 5 to 7. However, the quality of the spirit-levelling data remains a contributor to the distortions in the AHD.

The summary of the tilts and their significance (via the  $R^2$  value) in Table 2 are more telling. Both the north-south and east-west tilts decrease when the SST constraints are removed. The east-west tilts are both insignificant. More importantly, however, the north-south tilt and its significance are reduced substantially. This shows that SST is indeed a major contributor to the north-south tilt in the AHD over WA, as well as exaggerating the higher-order distortions. However, there are other distorting effects on the AHD that are not caused by the SST constraints. The quality, processing and geometry of the spirit-levelling observations is thus a remaining cause, and work is currently underway to try to isolate these.

## Summary and Conclusion

We have used a newer and reprocessed set of 243 GPS-derived ellipsoidal heights in a consistent reference frame and a GRACE-augmented version of AUSGeoid98 to assess the north-south tilt and higher-order distortions in the AHD over WA. Using published (official) AHD heights, the north-south apparent tilt is  $\sim 0.27$  mm/km ( $R^2=0.54$ ), but which reduces to  $\sim 0.018$  mm/km ( $R^2=0.37$ ) when the SST constraints are removed from a readjustment of the same spirit-levelling data. The east-west apparent tilts are insignificant ( $R^2=0.02$ ).

This shows that the MSL constraints applied to the AHD (1971) allow SST, which was not modelled at the time, to cause a north-south tilt in the AHD, as well as exacerbating the effect of spirit-levelling errors. While the tilt is seemingly small, it is now a known error that can be corrected in any future redefinition of the AHD. However, higher-order (regional) distortions remain, which must be due to other errors in the spirit-levelling data, which we are currently investigating.

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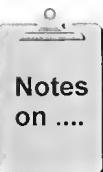
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**Table 2**Summary of latitudinal and longitudinal tilts of the residuals ( $\varepsilon$ ) and their significance by way of the R-squared value

Tilt	North-south	R-squared	East-west	R-squared
GPS-quasigeoid-AHD	$\sim 0.27$ mm/km	0.54	$\sim 0.07$ mm/km	0.02
GPS-quasigeoid-AHDnoSST	$\sim 0.18$ mm/km	0.37	$\sim 0.01$ mm/km	0.01

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## Range extension of the Western Heath Dragon, *Rankinia adelaidensis adelaidensis* (Squamata: Agamidae)

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**Abstract.** Two recent captures and a sighting of *Rankinia adelaidensis* increase its recorded geographical distribution in a southerly direction. In accordance with other recent range extensions recorded south of the Swan River, it is probable that the geographical distributions for other species will be extended into the southern coastal plain with further surveys.

**Key words:** Dragon lizards, geographic range, Western Australia, Swan coastal plain

### Introduction

The Mandurah, Dawesville and Yalgorup-Peel regions have been subject to substantial development pressure over the past few years. Current and planned developments within the region have seen the clearing of many remnant bushland patches on the outskirts of existing suburbs, and the clearing of smaller patches of remnant habitat within established suburbs. Vertebrate fauna surveys associated with environmental impact assessments (EIAs) for new developments have provided valuable information on terrestrial fauna located in the region.

Davis & Bamford (2005) reported the first record of *Lerista lineopunctulata* and second record of *L. lineata* from the Yalgorup area. Davis & Bamford (2005) suggested that further fauna work in the area may resolve the southerly distribution of other fossorial reptile species.

The Western Heath Dragon, *Rankinia adelaidensis*, is separated into two disjunct subspecies, *Rankinia a. adelaidensis* and *R. a. chapmani*. Storr *et al.* (1983) describe the distribution of *Rankinia a. adelaidensis* as 'midwest and lower west coasts of Western Australia, from a little north of the Murchison to a little south of the Swan River and inland to Coorow and Muchea' and *R. a. chapmani* as 'southern semiarid zones from Stirling Range east to Yorke Peninsula'. This range extension

relates to *R. a. adelaidensis* subspecies. This species was formally placed in the genus *Tympanocryptis adelaidensis* (Gray 1841), while Melville *et al.* (2001) suggested that it should be placed in *Ctenophorus*.

The habitat of *R. a. adelaidensis* was described by Bush *et al.* (1995; 2007) as low coastal vegetation on beaches and dunes, including heathlands and Banksia woodlands on the Swan Coastal Plain.

We report here two recent captures that are outside the published geographical distribution for this dragon but within known suitable habitat.

According to records in the Western Australian Museum database, the previous most southerly records of *R. a. adelaidensis* are from Jandakot (13 records), Yangebup, Gosnells and a single record from Caddadup Reserve, Mandurah. There is also a 1957 record from the south-west cape region at Deepdene in 1957 (R12427). Given the single record in 1957 and geographical isolation of the record, it is unknown whether it is a genuine record or an error in the database. Figure 1 indicates the recorded locations of *R. a. adelaidensis* in the WA museum collections and the extension to its published distribution represented by the three observations reported here.

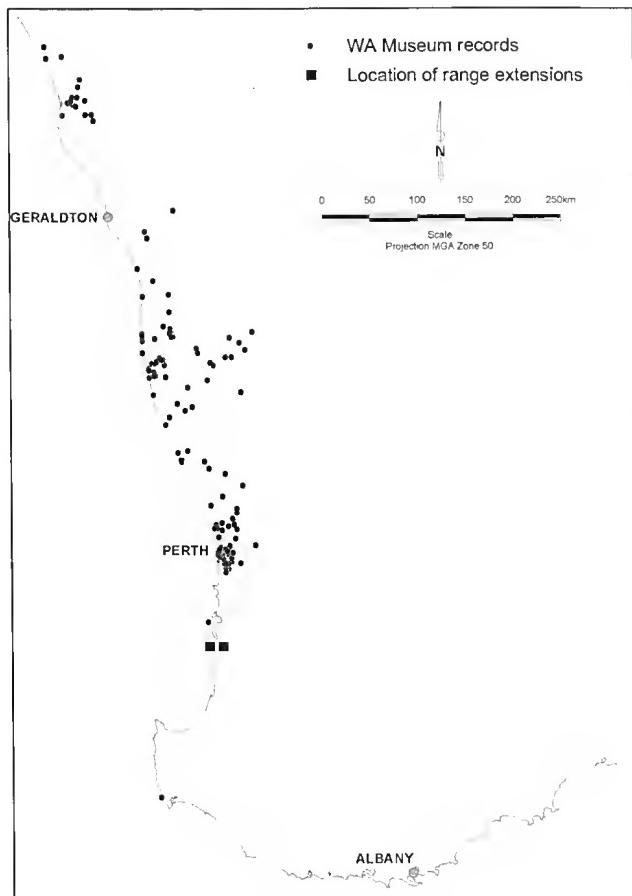


Figure 1. Location of specimens of *Rankinia a. adelaidensis* based on Western Australian Museum records, squares represent recent observations reported here.

## Observations

On 18<sup>th</sup> January 2007 two specimens were captured at Preston Beach (MGA 50 373356E 6364661N). The specimens were captured in funnel traps (Thompson & Thompson, 2007) as part of an EIA for a proposed development in the region. The habitat was coastal heath of *Agonis flexuosa*, *Spyridium globulosum* and *Acacia rostellifera* shrubland on coastal sand. Specimens were not vouchered with the WA Museum as they were confidently identified and released at the point of capture. In addition to the captures reported here, the authors are aware of another observation recently lodged with the WA Museum. This is shown in Figure 1 to the north of the two captures reported here.

## Discussion

Davis & Bamford (2005) reported an extension to the known distribution of *Lerista lineopunctulata* and *L. lineata* south of Perth. The range extension of *R. a. adelaideensis* reported here, combined with range extensions reported by Davis & Bamford (2005), raises the possibility of additional records of other Swan Coastal Plain fauna species currently known from north of the Swan River basin being recorded further south.

Given the development pressures currently being experienced in the Mandurah, Dawesville and Yalgorup-Peel regions, it is likely that fauna surveys conducted as part of EIAs in the region will extend the known distribution of some other species. The status of the Deepdene record requires clarification, possibly by surveying the location of this record.

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